Environmental Knowledge in the Banded Mongoose (*Mungos mungo*)

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Von

Corsin A. Müller

von

Bütschwil, SG

Promotionskomitee

Prof. Dr. Marta Manser (Vorsitz und Leitung der Dissertation)

Prof. Dr. Carel van Schaik

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Summary

Social carnivores are of particular interest in the study of cognition because complex social systems are thought to promote the evolution of specialized cognitive abilities and intelligence in general (social intelligence hypothesis). Most research on cognition in animals has focused on primates as our closest relatives, and experiments were commonly conducted with captive animals. This approach has produced some impressive results but it suffers from several limitations. First, the social intelligence hypothesis posits that cognitive abilities are related to complex social lives rather than restricted to particular taxa. Second, studies on cognition with captive animals using artificial tasks may report misleading results because these tasks are not relevant under natural conditions. Therefore, I explored basic cognitive abilities of free-ranging banded mongooses (*Mungos mungo*), small social carnivores, in their natural habitat in Queen Elizabeth National Park, Uganda.

With translocations of scent marks, I demonstrated that banded mongooses discriminate between members of their own group and foreigners, between neighbours and strangers and between different neighbouring groups solely based on scent. In contrast to many studies in solitary animals, I found that banded mongooses responded more intensely to scent marks of neighbours than strangers (the opposite of the 'dear enemy' effect). I argue that this is related to cooperative territory defence and to different threats posed by neighbours and strangers. Furthermore, my experiments showed that banded mongooses extract information about sex, age, dominance and reproductive status of the sender from scent marks, and that one of the main functions of scent-marking in this species lies in intrasexual competition. This is, I argue, a consequence of both sexes commonly breeding in their natal group. In a second experiment, I explored cognitive abilities required for the banded mongooses' cooperative breeding system. Banded mongoose pups form stable and exclusive associations with particular providers (their 'escorts'). With removal experiments and subsequent playbacks, I demonstrated that pups and escorts recognize each other solely on the basis of their individually distinct vocalizations, and that both parties contribute to the maintenance of these associations. Finally, I performed playback experiments to show that banded mongooses recognize and appropriately respond to heterospecific alarm calls. However, banded mongooses did not respond according to the urgency level encoded in these calls, a contrast to some recent studies, which showed that animals can extract referential information from heterospecific alarms. These findings have important implications for the understanding of how recognition of heterospecific signals is acquired.

My thesis shows what specific information banded mongooses extract from their environment, but it also provides examples of available information that is not used. I discuss these findings with regard to limitations of the sensory and cognitive apparatus and to the relevance of information in particular situations. I further discuss the use of information and the associated cognitive abilities in the context of demands of the ecological and social environment.

Zusammenfassung

Soziale Raubtiere sind für die Kognitionsforschung besonders interessant, da komplexe Sozialsysteme die Evolution von speziellen kognitiven Fähigkeiten und von Intelligenz im Allgemeinen begünstigt haben könnten (‚social intelligence' Hypothese). Forschung über kognitive Fähigkeiten hat sich hauptsächlich mit Primaten beschäftigt, da diese unsere nächsten Verwandten sind. Zudem wurden Experimente meist mit in Gefangenschaft gehaltenen Tieren durchgeführt. Dieser Ansatz hat zwar zu einigen eindrücklichen Ergebnissen geführt, ist jedoch in mehrfacher Hinsicht limitierend. Einerseits besagt die ‚social intelligence' Hypothese, dass kognitive Fähigkeiten vor allem die Folge einer sozialen Lebensweise, und nicht auf bestimmte Tiergruppen beschränkt sind. Andererseits können Experimente mit in Gefangenschaft gehaltenen Tieren irreführende Resultate liefern, weil die in den Experimenten gestellten Aufgaben unter natürlichen Bedingungen nicht relevant sind. Daher habe ich grundlegende kognitive Fähigkeiten von freilebenden Zebramangusten (*Mungos mungo*), einer kleinen sozialen Raubtierart, in ihrem natürlichen Lebensraum im Queen Elizabeth Nationalpark, Uganda studiert.

Durch das Versetzen von Geruchsmarkierungen (Kot und Urin) konnte ich zeigen, dass Zebramangusten am Geruch nicht nur Mitglieder der eigenen Gruppe von anderen Artgenossen unterscheiden können, sondern auch zwischen verschiedenen Nachbargruppen sowie zwischen Nachbarn und Fremden. Solitär lebende Vertebraten sind häufig weniger aggressiv gegenüber Nachbarn als Fremden (‚dear enemy' Effekt). Zebramangusten zeigten jedoch eine intensivere Reaktion gegenüber Geruchsproben von Nachbarn als von Fremden, was durch die soziale Lebensweise und die gemeinschaftliche Verteidigung des Territoriums bedingt sein kann, sowie durch unterschiedliche Gefahren, die von Nachbarn und Fremden ausgehen. Weiter haben meine Experimente gezeigt, dass Zebramangusten aus Geruchsmarkierungen Information über Geschlecht, Alter, Dominanz- und Fortpflanzungsstatus gewinnen, und dass diese Markierungen eine wichtige Rolle bei der intrasexuellen Konkurrenz um Fortpflanzung spielen. Dies ist wahrscheinlich die Folge des besonderen Sozialsystems der Zebramangusten, bei welchen sich sowohl Männchen als auch Weibchen häufig in der Geburtsgruppe fortpflanzen.

In einem zweiten Experiment untersuchte ich kognitive Fähigkeiten, die bei der kooperativen Jungenaufzucht eine Rolle spielen. Bei Zebramangusten bilden Jungtiere individuelle und exklusive Beziehungen mit einem bestimmten Versorger, einem sogenannten ‚escort'. Ich habe kurzfristig Jungtiere oder deren ‚escorts' aus der Gruppe entfernt und Playback-Experimente durchgeführt. Auf diese Weise konnte ich zeigen, dass sich Jungtiere und ‚escorts' gegenseitig anhand ihrer individuellen Rufe erkennen, und dass sowohl die Jungtiere als auch die ‚escorts' aktiv zur Aufrechterhaltung dieser Verbindungen beitragen.

In einem dritten Experiment habe ich Zebramangusten Alarmrufe anderer Arten vorgespielt und konnte zeigen, dass die Tiere diese Rufe erkennen und mit angemessenem Räubervermeidungsverhalten darauf reagieren. Die Zebramangusten reagierten jedoch nicht entsprechend der in den Alarmrufen kodierten Dringlichkeit, was im Gegensatz zu anderen Studien steht, die gezeigt haben, dass Tiere referentielle Information aus artfremden Alarmrufen gewinnen können. Diese Erkenntnisse haben wichtige Implikationen für das Verständnis, wie die Erkennung von Signalen anderer Arten erfolgt.
Meine Dissertation zeigt, welche Informationen Zebramangusten aus ihrer Umwelt entnehmen, aber auch welche an sich verfügbare Information von ihnen nicht genutzt wird. Ich diskutiere diese Erkenntnisse hinsichtlich Grenzen des sensorischen und kognitiven Systems, und hinsichtlich der situationsabhängigen Relevanz bestimmter Informationen. Weiter diskutiere ich meine Ergebnisse im Zusammenhang von spezifischen Gegebenheiten der ökologischen und sozialen Umwelt, welche die Nutzung von Information und die dazugehörigen kognitiven Fähigkeiten fördern.

GENERAL INTRODUCTION

General Introduction

Ueberhaupt aber geht es mit der geistigen Nahrung nicht anders, als mit der leiblichen: kaum der funfzigste Theil von dem, was man zu sich nimmt, wird assimilirt: das Uebrige geht durch Evaporation, Respiration, oder sonst ab.

Arthur Schopenhauer (1851)

Free-living animals face a challenging environment in which they need to find food, mates and shelter and at the same time avoid predators, competitors and unfavourable weather conditions. The environment provides a vast amount of information, some of which can help to tackle the tasks mentioned above, and much of which is irrelevant. The ecological and social environment promotes the use of information which increases survival and reproduction, and influences the evolution of cognitive abilities required for that. However, at the same time constraints of the receiver's sensory and cognitive apparatus limit what information can be perceived and processed. Here I investigate what information free-ranging banded mongooses, small social carnivores, extract from their environment in the context of these advancing and limiting factors.

Limits to the use of information

Healthy humans can hear sounds at frequencies between 20 Hz and 20 kHz, whereas the hearing range extends up to 40 kHz for carnivores (Kelly et al. 1986), and even further for some rodents, bats and whales (Thomas et al. 1988; Neuweiler 1990; Heffner et al. 2001). Similarly, also frequency resolution, temporal resolution and perception of frequency modulation are limited (Bradbury & Vehrencamp 1998). The limits to olfactory perception are less well explored. Silk moth males for example can detect as little as 200 molecules of their females' sexual pheromone (Kaissling & Priesner 1970) and mice can distinguish between urine of congenic strains differing by a single

gene (Yamazaki et al. 1983). Low sensitivity in a particular task is either explained by a trade-off with enhanced sensitivity in another area, or by high costs of developing and maintaining a perception system, which exceed the benefits of the additional information that would get accessible (Bradbury & Vehrencamp 1998). Such constraints have the consequence that a receiver's use of the available information is less than optimal (Shettleworth 2001).

Within the range of perception, sensory filters further reduce the amount of information processed by filtering out the irrelevant background and focussing on relevant information. Contrasts for example are accentuated, repeated stimuli are ignored and novel stimuli elicit stronger responses (Young 1989). Sensitivity usually varies greatly within the range of perception and is highest in the most relevant area (e.g. Fullard 1987; Sumner & Mollon 2000). Furthermore, the sensory system can focus on detecting particular patterns (visual, olfactory or acoustic 'search images'; Pietrewicz & Kamil 1979; Nams 1991), and selective attention to a single pattern is more efficient than divided attention between several patterns (Zentall 2005).

Even information that passed the sensory filters may often not lead to any change in the receiver's behaviour (thus Schopenhauer's conclusion that with intellectual as with corporal food only a small proportion gets assimilated). Depending on the context, a particular piece of information may be of relevance or not. For example, some songbirds use special song types to address receivers of one sex in particular (Rehsteiner et al. 1998; Kunc et al. 2006). The use of information further requires interpretation of the same, and the mechanism by which interpretation is achieved may constrain whether and how information is used. Where the use of information is acquired by learning (individual or social), the interpretation can change and become more accurate and complete as it is updated with experience. For instance, animals can learn to extract referential information from alarm calls (Hauser 1988; Zuberbühler 2000b; Hollén & Manser 2006). Where it is innate on the other hand, the interpretation is not influenced by the individual's experience. Therefore, events occurring only rarely in an individual's lifetime may not be incorporated, even though they could make the interpretation of the same piece of information more accurate.

Environmental knowledge in free-ranging social mammals

Cognitive research with captive animals has a long and successful tradition (reviewed in: Shettleworth 1998; Heyes & Huber 2000). However, recent findings stress the importance of incorporating an animal's environment and the challenges it faces under natural conditions into research on cognitive abilities. Chimpanzees and rhesus monkeys for example perform less well in cooperative than in competitive, more natural tasks (Hare et al. 2001; Hare & Tomasello 2004; Flombaum & Santos 2005) and wild New Caledonian crows seem to use a different strategy than captive ones to solve the same problem (Hunt et al. 2006). On the other hand, cognitive skills found in captive studies are sometimes not reproducible in wild animals (e.g. Gajdon et al. 2004; Halsey et al. 2006). This may be because, for animals facing the challenges of their natural environment, these skills are traded off for other, more relevant activities such as predator avoidance. Adapting experimental setups for studies on captive animals is one way to test animals' cognitive abilities in a more natural context. However, this approach has its obvious limits since semi-natural settings in captivity cannot fully match natural conditions. Therefore, research on cognitive abilities of free-ranging animals has its clear advantages and, even though logistically challenging, this approach has led to some impressive results including referential communication in vervet monkeys (Seyfarth et al. 1980a, 1980b), Diana monkeys (Zuberbühler 2000a, 2000c) and meerkats (Manser 2001; Manser et al. 2001), recognition of third-party relationships in baboons (Cheney et al. 1995; Cheney & Seyfarth 1999) and spotted hyenas (Engh et al. 2005), causal inference in rhesus monkeys (Hauser & Spaulding 2006), and episodic-like memory in rufous hummingbirds (Henderson et al. 2006).

Surviving in a natural environment comes with a variety of challenges which can be mastered with appropriate cognitive abilities. Complex tasks, for example in regard to foraging, are thought to have promoted specialized cognitive abilities, which are sometimes summarized under the term 'ecological intelligence' (sensu Milton 1988) or, when dealing with extractive foraging in particular, 'technical intelligence' (Byrne 1997). For example, episodic-like memory has been favoured in food-caching corvids, which need to remember what type of food (perishable or non-perishable) they stored where and when (Clayton & Dickinson 1998) and hummingbirds demonstrated similar abilities when remembering which flowers they had visited when (Henderson et al. 2006). Furthermore, primates and great apes in particular (Byrne 1997; Hauser & Spaulding

2006), but also keas (Huber & Gajdon 2006) solve complex tasks when extracting hidden or defended food sources, which may have favoured tool use and means-end comprehension, a primitive form of causal reasoning.

Social animals face challenges exceeding those of solitary animals. Hence it has been suggested that a complex social environment represents a selection pressure favouring the evolution of cognitive abilities (social intelligence hypothesis; Jolly 1966; Byrne & Whiten 1988). For example, social life has been related to neocortex size in primates and other mammals (Dunbar 1992, 1995; Barton 1996; Dunbar & Bever 1998; but see Beauchamp & Fernandez-Juricic 2004; Lindenfors 2005), and lives in complex individualized societies are thought to have promoted social skills and the cognitive abilities required for them in an evolutionary arms race (Zuberbühler & Byrne 2006). Also, successful strategies for particular tasks in a social life require appropriate cognitive abilities. For example, while living in groups may have a variety of benefits, it often comes with increased competition for food and mates (Alexander 1974). In complex societies, in which individuals are discriminated, this may have promoted the ability to take the perspective of conspecific competitors, as has been demonstrated in great apes (Hare et al. 2000; 2001) as well as in food-caching corvids (Emery & Clayton 2001; Bugnyar & Heinrich 2005; Dally et al. 2006). Furthermore, particularly in social groups with kin-based social networks, individuals can increase their reproductive success by forming coalitions or alliances (Harcourt & de Waal 1992). This probably promoted the ability to recognize third-party relationships, as has been demonstrated in primates as well as in a carnivore with a similar social system (vervet monkeys: Cheney & Seyfarth 1980; baboons: Cheney et al. 1995; Cheney & Seyfarth 1999; bonnet macaques: Silk 1999; white-faced capuchin monkeys: Perry et al. 2004; spotted hyenas: Engh et al. 2005). It is therefore of particular interest to study cognition in animals with complex social systems such as the banded mongoose, a small (< 2 kg) carnivore. This species has been studied mostly in regard to its unusual reproductive behaviour (e.g. Cant 2000; Gilchrist 2004; Hodge 2005), but little in regard to cognition. While I do not address higher cognitive abilities such as causal reasoning, referential communication or recognition of third-party relationships here, I explore basic cognitive abilities that are related to the banded mongooses' social behaviour.

Study species

Banded mongooses face a number of cognitive challenges that are related to their environment and their social system. Contrary to most species of the family Herpestidae, banded mongooses are social and diurnal. Similar to baboons and spotted hyenas, which are thought to feature one of the most complex social systems known in the animal kingdom (Holekamp 2007), banded mongooses live in multi-male-multi-female groups of 5 to 60 individuals (Fig. 1), including multiple generations and several matrilines (Cant 2000). However, unlike baboons and hyenas, they do not normally form subgroups, alliance-formation is not known and positions in the rather shallow dominance hierarchies are probably not 'inherited' from the mother. Nevertheless, banded mongooses are confronted with many of the same tasks other social mammals are facing. I investigated how mongooses deal with some of these tasks and what cognitive abilities are involved in their strategies.

While banded mongooses compete within groups for access to food and mates, they also cooperate in competition between groups for space and access to mates (Cant et al. 2002). Banded mongoose groups are formed either when a single-sex splinter group is joined by an opposite-sex splinter group, or when a single-sex splinter group takes over a small group, chasing away their same-sexed rivals (Gilchrist 2001; Cant et al. 2001). Such splinter groups disperse from their original groups via eviction by co-residents, displacement by immigrants, or voluntary emigration. Not only can residents of a small group be permanently displaced by same-sexed rivals from neighbouring groups, aggressive interactions between groups are also common and often result in fierce fights with sometimes fatal consequences to members of the inferior group (Rood 1975; Cant et al. 2002). Since neighbouring groups on the one hand pose a threat depending on their group size, but on the other hand may also offer options for dispersal and extra-group matings, the monitoring of neighbouring groups' sizes and composition as well as of their females' oestrus state probably has positive fitness consequences. For this, recognition of different categories of conspecifics on group level is required.

Unlike in most mammals, both male and female banded mongooses breed regularly in their natal group and matings between close relatives are not exceptional (Cant 1998; Gilchrist 2001). Reproductive skew is generally low with up to 10 females breeding concurrently and synchronously (Cant 2000). Banded mongooses cooperate in the rearing of young (Cant 2003; Gilchrist 2004; Hodge 2005). Non-breeding individuals

contribute substantially to rearing the group's pups by babysitting in the first 3 to 4 weeks after birth of the litter (Rood 1974; Cant 2003) and by provisioning for another 6 to 8 weeks thereafter. During this period, most pups form exclusive associations with individual providers, their 'escorts' (Gilchrist 2004; Hodge 2005). This requires individual recognition and may represent the basis of an individually structured society.

Banded mongooses are susceptible to predation by a large number of natural enemies and predator avoidance is therefore of prime importance in a mongoose's life. While foraging, groups may spread out considerably and temporary group splits have been observed on a number of occasions, particularly in one pack during dry seasons (pers. obs.). Unlike meerkats (Clutton-Brock et al. 1999; Manser 1999), banded mongooses rarely mount sentinels during foraging (Bell 2006), possibly because nearby bushes offer cover and restrict vision even for raised individuals. Like meerkats, banded mongooses use alarm calls to warn group members from approaching predators. However, predator avoidance is probably more efficient if alarms of other sympatric species are also recognized, and banded mongooses have been observed responding to alarms of a variety of sympatric birds, including crowned plovers, Senegal plovers, spurwinged plovers, wattled plovers, helmeted guineafowl, red-necked spurfowl and arrow-marked babblers (pers. obs.).

Study site

The data presented in this thesis were collected between February 2004 and October 2005 in Queen Elizabeth National Park, Uganda. The study population consisted of nine groups of banded mongooses on and around Mweya Peninsular (0°12' S, 29°54' E). All individuals were marked, either with colour-coded plastic collars or with small shaves on the rump (for details see Cant 2000) and at least one adult per group was fitted with a radiocollar. The banded mongoose population on Mweya Peninsular was first studied by Jon Rood in the early 1970ies (Rood 1974; Rood 1975) and then again continuously from 1994 onwards by a suite of PhD students (Cant 1998; De Luca 1998; Gilchrist 2001; Hodge 2003; Bell 2006). I was lucky to have access to a more or less complete life-history database compiled by my predecessors covering the last 10 years. Apart from that, all data presented in this thesis are results of my own research.

Figure 1. Banded mongoose group having a siesta in the shade.

Figure 2. Section of Mweya Peninsular with Lake Edward in the background. Other parts of the study area are more open.

Figure 3. Some of the top predators present in the study area: lion, leopard, African fish eagle, and rock python.

The habitat in the study area is a semi-arid (annual precipitation 800-1000 mm; Rood 1975; Gilchrist 2001) short-grass savannah dotted with numerous thickets (*Capparis tomentosa, Azima tetracantha*) and Euphorbian trees (*Euphorbia candelabrum*; Fig. 2) (Lock 1993). Temperature fluctuates only little throughout the year (mean daily temperature 23-26 °C; Cant 1998; Gilchrist 2001) and some rain falls in all months. However, rainfall typically peaks in March-May and September-November with two intervening dry seasons in January/February and June/July (Rood 1975). The banded mongooses share the habitat with large herbivores (Elephant, Buffalo, Hippopotamus, waterbuck, bushbuck, Uganda kob, warthog and giant forest hog), some in contrast to banded mongooses solitary and nocturnal herpestids (white-tailed mongoose, Egyptian mongoose) and a vast number of bird species. Potential predators include large carnivores

(lion, leopard, spotted hyena), raptors (martial eagle, black-chested snake eagle, steppe eagle, African marsh harrier) and reptiles (monitor lizard, rock python). Additionally, pups are predated regularly by marabou storks.

Outline of thesis

In this thesis, I investigate what information banded mongooses extract from their environment in situations that are related to aspects of their social system or their ecological environment. I touch on communication between and within groups as well as on eavesdropping (sensu McGregor 1993) on heterospecific communication. In the first chapter, I explore olfactory communication between territorial banded mongoose groups. I focus in particular on the discrimination between the own group, neighbouring groups and strangers, and on the threat levels represented by different opponents. While relationships between territorial neighbours have been widely studied in solitary animals, social species have been neglected. I show how living in groups, in which individuals cooperate in competition against neighbours, can turn relationships between neighbours from tolerance to open hostility. In Chapter 2, I turn the attention to other functions of scent-marking in communication between and within groups. I test several hypotheses for the function of scent-marking in communication related to sexual behaviour and argue that peculiar social systems, as found in the banded mongoose, may influence the main function of scent-marking in a species. The second half of the thesis deals with acoustic communication. In Chapter 3, I investigate vocal communication within groups between dependent pups and their providers. The unusual pup care system exhibited by banded mongooses offers a good opportunity to test for individual recognition between pups and adults in a cooperatively breeding species. This ability is relevant for cooperative breeding theory but has rarely been demonstrated. The experimental approach I used further allows verifying earlier findings based on observational data in regard to the maintenance of the associations between pups and providers. Chapter 4 explores interception of communication among individuals of different species. While eavesdropping on heterospecific communication is known to occur widely, little effort has been put into studying what animals learn by doing so. I investigate what information banded mongooses extract from alarm calls of sympatric birds. I suggest that the extraction of specific information from heterospecific vocalizations is related to the

mechanism by which recognition of these calls is acquired, particularly opposing innate and learned recognition. In the final chapter, I discuss my findings in the context of cognitive limitations to the use of available information and in relation to the banded mongooses' social and ecological environment.

This study provides data on basic cognitive abilities in a social carnivore, a taxon that is of particular interest but underrepresented in the study of cognition (Zuberbühler & Byrne 2006). Rather than focussing on social intelligence only, I studied cognitive abilities in relation to both the social and the ecological environment, an approach that has been advocated since social and non-social demands on cognition interact (Holekamp 2007). My thesis has a strong focus on an experimental approach to research on basic cognitive abilities of free-ranging animals under natural conditions. This approach suffers from limitations and logistic difficulties compared to experiments conducted with captive animals or under semi-natural conditions. Nevertheless it is a valuable if rarely taken approach to cognitive research as well as an important complement to cognitive research by observation of free-ranging animals in their natural habitat.

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Appendix

Scientific names of the species mentioned in this chapter

MAMMALIA

African elephant	*Loxodonta africana*
Banded mongoose	*Mungos mungo*
Bonnet macaque	*Macaca radiata*
Bushbuck	*Tragelaphus scriptus*
Cape buffalo	*Syncerus caffer*
Baboon	*Papio hamadryas/cynocephalus*
Chimpanzee	*Pan troglodytes*
Common marmoset	*Callithrix jacchus*
Diana monkey	*Cercopithecus diana*
Domestic cat	*Felis catus*
Egyptian mongoose	*Herpestes ichneumon*
Giant forest hog	*Holochoerus meinertzhageni*
Hippopotamus	*Hippopotamus amphibius*
Leopard	*Panthera pardus*
Lion	*Panthera leo*
Meerkat	*Suricata suricatta*
Rhesus monkey	*Macaca mulatta*
Spotted hyena	*Crocuta crocuta*
Uganda kob	*Kobus kob*
Vervet monkey	*Cercopithecus aethiops*
Warthog	*Phacocoerus aethiopicus*
Waterbuck	*Kobus ellipsiprymnus*
White-faced capuchin monkey	*Cebus capucinus*
White-tailed mongoose	*Ichneumia albicauda*

AVES

African fish eagle	*Haliaeetus vocifer*
African marsh harrier	*Circus ranivorus*
Arrow-marked babbler	*Turdoides jardineii*
Black-chested snake eagle	*Circaetus pectoralis*
Crowned plover	*Vanellus coronatus*
Helmeted guineafowl	*Numida meleagris*
Kea	*Nestor notabilis*
Marabou stork	*Leptoptilos crumeniferus*
Martial eagle	*Polemaetus bellicosus*
New Caledonian crow	*Corvus moneduloides*
Red-necked spurfowl	*Francolinus afer*
Rufous hummingbird	*Selasphorus rufus*
Senegal plover	*Vanellus lugubris*
Spurwinged plover	*Vanellus spinosus*
Steppe eagle	*Aquila nipalensis*
Wattled plover	*Vanellus senegallus*

REPTILIA

Monitor lizard	*Varanus niloticus*
Rock python	*Python sebae*

INSECTA

Silk moth	*Bombyx mori*

CHAPTER 1

'Nasty neighbours' rather than 'dear enemies' in a social carnivore

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'Nasty neighbours' rather than 'dear enemies' in a social carnivore

Corsin A. Müller & Marta B. Manser

Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

ABSTRACT

Territorial animals typically respond less aggressively to neighbours than to strangers. This 'dear enemy effect' has been explained by differing familiarity or by different threat levels posed by neighbours and strangers. In most species, both the familiarity and the threat-level hypotheses predict a stronger response to strangers than to neighbours. In contrast, the threat-level hypothesis predicts a stronger response to neighbours than to strangers in species with intense competition between neighbours and with residents outnumbering strangers, as commonly found in social mammals such as the banded mongoose (*Mungos mungo*). The familiarity hypothesis predicts reduced aggression towards neighbours also in these species. We exposed free-living banded mongoose groups to translocated scent marks of neighbouring groups and strangers. Groups vocalized more and inspected more samples in response to olfactory cues of the neighbours than to the strangers. Our results support the threat-level hypothesis and contradict the familiarity hypothesis. We suggest that increased aggression towards neighbours is more common in social species with intense competition between neighbours, as opposed to reduced aggression towards neighbours typical for most solitary species.

1. INTRODUCTION

Relationships between territorial competitors are commonly explained by two hypotheses, both of which are based on the observation that many territorial animals respond less aggressively to neighbours than to strangers (reviewed in Ydenberg et al. 1988; Temeles 1994), a phenomenon termed the 'dear enemy effect' (sensu Fisher 1954). First, the familiarity hypothesis argues that, when the relationship between neighbours is settled, reduced aggression towards each other allows conservation of time and energy and reduces the risk of injuries (Wilson 1975), for example, because familiarity reduces the likelihood of role mistakes in territorial contests (Ydenberg et al. 1988). It has also been suggested that residents engage in fights with strangers to gather information about them (Getty 1989). Much evidence has accumulated in support of the familiarity hypothesis (reviewed in Ydenberg et al. 1988; Temeles 1994). In some species, however, the response to neighbours is more intense than the response to strangers (5 out of 55 species reviewed in Temeles 1994) and territory holders may increase aggression towards familiar but untrustworthy neighbours (Godard 1993; Olendorf et al. 2004), suggesting that aggression is not always reduced towards more familiar individuals.

Second, the threat-level hypothesis argues that neighbours and strangers may compete for different resources and, therefore, represent different levels of threat to an established territory holder. The response of residents should, thus, be stronger to the category of conspecifics that represents the bigger threat (Temeles 1994). Strangers often represent 'floaters' looking for a territory (Wilson 1975), and may thus be competitors for both territories and mates, whereas neighbours may only compete for mates. In this situation, both the familiarity hypothesis and the threat-level hypothesis predict a more aggressive response to strangers than to neighbours.

Studies contrasting the familiarity and the threat-level hypotheses are scarce, even though neighbour-stranger discrimination (NSD) has been demonstrated in a variety of taxa, including birds, mammals, reptiles and amphibians (reviewed in Ydenberg et al. 1988; Temeles 1994). Solitary northern harriers (*Circus cyaneus*), for example, defend feeding territories and respond more aggressively to neighbours than to strangers (Temeles 1990). In this species, neighbours may usurp portions of residents' territories, whereas floaters primarily appear to steal food and were never observed to take over

territories. The pattern of NSD observed in northern harriers contradicts the familiarity hypothesis.

We suggest that the familiarity and the threat-level hypotheses can be contrasted by studying neighbour recognition in social vertebrates, which have been largely neglected in this regard (Radford 2005). In group-living species, differences in the value of contested resources might not be sufficient to explain the threat levels of neighbours and strangers. An additional parameter is relevant: group size of neighbours and strangers relative to resident groups. Many social animals commonly disperse singly or in small numbers, and pose little threat to larger established groups (Wilson 1975). In contrast, relationships between neighbouring groups of territorial animals are often aggressive. Groups may attempt to expand their territory at the expense of neighbouring groups (Mech & Boitani 2003), and some social mammals engage in fights with neighbouring groups, leading to serious injuries and occasional fatalities (Schaller 1972; Goodall 1986; Mech & Boitani 2003). Thus, neighbours may pose a significant threat to groups defending a territory, whereas strangers are generally outnumbered by established territory holders.

We experimentally tested the threat-level and the familiarity hypotheses in the banded mongoose (*Mungos mungo*), a small (less than 2 kg), territorial, cooperatively breeding carnivore. Banded mongoose groups are stable units formed either when a single-sex splinter group is joined by an opposite-sex splinter group, or when a single-sex splinter group takes over a small group, chasing away their same-sexed rivals (Cant et al. 2001). Such splinter groups disperse from their original groups via eviction by co-residents, displacement by immigrants or voluntary emigration. Home ranges may overlap considerably and borders are demarcated by faeces, urine and secretions of the anal glands (Rood 1975; C. A. Müller 2005, personal observation), which are inspected intensively when encountered by neighbours. Group sizes in banded mongooses vary over a large scale (range 5-44 individuals, mean 20 individuals; Cant 2000), and groups may expand their home ranges at the expense of smaller neighbouring groups (Rood 1975; and see electronic supplementary material). Competition between groups is intense, resulting in inter-group encounters with sometimes fatal consequences to members of the inferior group (Rood 1975; Cant et al. 2002; Gilchrist & Otali 2002). Strangers, in contrast, represent single individuals or splinters that disperse up to 20 km (Cant et al. 2001) and probably cross several established territories in the process. These splinters are commonly small (interquartile range=2-6.5, N=28; Banded Mongoose Project 2005,

unpublished data), are outnumbered by resident groups and, thus, pose little threat to them. This is also the case when considering that single-sex splinters may compete only with their same-sexed rivals in resident groups when they attempt to take over. In the six documented group takeovers between 1998 and 2005, only small groups with no more than two residents of one sex were affected (Banded Mongoose Project 2005, unpublished data). This indicates that already groups of moderate size are at low risk of takeovers.

The familiarity and the threat-level hypotheses make contrasting predictions in banded mongooses. The familiarity hypothesis predicts that resident groups respond more intensely to strangers than to neighbours. The threat-level hypothesis predicts that residents react more strongly to neighbours than to strangers. Both hypotheses also predict that residents further discriminate between different neighbouring groups, an ability that has been demonstrated in a subset of the species that show NSD (Cheney & Seyfarth 1982; Davis 1987; Stoddard 1996). The familiarity hypothesis predicts neighbour-neighbour discrimination if reduced aggression towards neighbours is based on reciprocation (Godard 1993). The threat-level hypothesis predicts more intense responses to larger than to smaller neighbouring groups. The ability to discriminate both between neighbours and strangers and between different neighbours has rarely been tested in group-living species.

We tested these predictions using scent-mark translocation experiments. In addition, we used repeated exposures to scent marks of strangers to test if banded mongoose groups habituate to olfactory stimuli of unfamiliar groups. Since we presented secondary cues, we could not measure aggressivity of the response directly. Instead, we used worry-calling propensity, counter-marking propensity and inspection as measures of response intensity. Worry calls are harmonic calls with a fundamental frequency between 0.4 and 0.7 kHz and most of the energy concentrated between 0.4 and 2.0 kHz (for spectrogram see electronic supplementary material). They occur singly or in sequences of several calls and they are given when mongooses encounter secondary cues of other mongooses or of predators and commonly result in recruitment of other group members (C. A. Müller 2005, personal observation; see electronic supplementary material, video). They have not been observed in any non-threatening context. We assumed that they reflected how unsettling the stimuli were to the inspecting animals, as in sciurids, for example, calling propensity is correlated with level of danger (Swaisgood et al. 1999) and with faecal glucocorticoid levels (Blumstein et al. 2006). Inspection behaviour was

assumed to be influenced by the familiarity of the stimulus, but it may also reflect gathering of additional information about the counterparts such as reproductive state of females, age and health (Sliwa & Richardson 1998; Swaisgood et al. 2002; White et al. 2003).

2. MATERIALS AND METHODS

This study was conducted on a wild population of individually marked banded mongooses in Queen Elizabeth National Park, Uganda (0°12' S, 29°54' E) between April 2004 and August 2005. The study population remained largely constant in size throughout this period and consisted of 210-240 individuals in nine groups, seven of which were habituated to close observation and included in the experiments described below. The size of these seven groups ranged from 8 to 44 individuals. Animals were classified in age classes as adults (greater than 12 months), subadults (6-12 months) and infants (less than six months). Date of birth was known for all individuals except for nine adult immigrants. All animals were trapped on a regular basis to refresh individual marks (colour-coded plastic collars or small shaves on the rump), detect pregnancies, take morphometric measures and estimate ectoparasite load (see Cant 2000 for details). For trapping as well as for scent-mark presentations, small amounts of bait were used (a mix of rice and gravy).

Life-history data were collected during daily visits to the groups. For all visits, we recorded location (Magellan GPS Companion and Garmin GPS 12) and occurrence of births and deaths to monitor changes in the size of groups and their home ranges. Additionally, we recorded all events of encounters between neighbouring groups (two groups which occupy adjacent territories) and between resident groups and floaters (animals not defending a territory but travelling singly or in small numbers over large distances).

(a) Scent-mark translocation experiments

In separate trials, each group was presented with excreta collected from four different donor groups: two neighbouring groups, a non-neighbouring group ('strangers')

and the group itself ('own group'). In a control condition prior to each experiment, the subject groups were exposed to fresh samples of herbivore faeces (warthog (*Phacochoerus aethiopicus*) or waterbuck (*Kobus ellipsiprymnus*)) and samples of water (1 ml with a spoonful of soil) to control for variable scent-marking and worry-calling propensity. The scent marks of each group were presented in two different locations in separate trials: the centre and the border of the experimental group's territory. Home ranges were divided into border and centre areas based on sightings recorded by GPS over the preceding 12 months. To test for discrimination between different neighbours, we presented scent marks of the neighbouring groups at the shared border as well as at the border with a different group (opposite border). To test for NSD, only the experiments at the shared border and in the centre were used. Experiments on the same group were spaced at least 14 days apart to minimize carry-over effects.

For each trial, six or seven samples of fresh scat and urine were collected from the donor group within 1 h. The set of scent marks consisted of scat and urine samples from 5 to 7 individuals (4-7 adults and 0-3 subadults and infants) and included samples of adult males and adult females and of both excretion types. Only samples with known identity of the excreting animal were used. If insufficient samples were collected ad libitum, we trapped several individuals and collected excreta from the traps. This procedure represented only minimal stress, since all individuals in the study population have been trapped on a regular basis (2-4 times a year) and they are used to it (Cant 2000). All animals were released within 15 min of trapping. This is well below the delay time between peak of hormones in the blood and in the faeces for mammals (Palme et al. 2005). However, we cannot exclude the possibility that faecal samples collected by trapping were more or less likely to include secretions from the anal glands (Asa et al. 1985). Less than 20% of all the samples were collected by trapping, and collection did not differ systematically between donor categories.

The collected samples were stored on ice and presented to the experimental group on the same day (on average 2 h after collection). Since banded mongooses often use open patches for territorial marking (C. A. Müller 2005, personal observation), the samples were arranged in a circle on open ground (spaced apart 30-50 cm). This enabled accurate observation of the mongooses' response from 5-10 m distance. We scattered 20-50 g of bait in a circle at 2-4 m distance to the samples to make sure that the mongooses would find the presented stimuli. The experiments were recorded for later analysis using a digital video camera (Panasonic NV-GX7) and a Sennheiser ME 66/K6 directional

microphone. Recording was stopped when no individual had approached any of the presented samples for 60 s.

The following response variables were evaluated: (i) number of individuals emitting worry calls; (ii) number of individuals counter-marking; and (iii) number and duration of inspection bouts (nose within 1 cm of a sample). Data on different types of counter-marks were pooled (urinating, defecating and anal marking). The duration of inspection bouts (one individual inspecting one sample) was determined frame-by-frame in Windows Movie Maker (1 frame=0.08 s). Only responses of adults were included in the analyses presented here, since younger individuals may not have learned to recognize neighbours yet.

To investigate how strangers become neighbours, we simulated the settling of a new group by repeatedly presenting scent marks of an unfamiliar (non-neighbouring) group to experimental groups. Six groups were exposed to scent marks of an unfamiliar group four times in a row (separated by 3-5 days). The experimental protocol was the same as described above. For the second, third and last experiments in these series, at least two samples were from individuals that had contributed to the set of samples earlier in the series. This allowed the experimental group to recognize the presented samples as from the same group, even if scent marks of banded mongooses do not contain group-specific information (Brown & MacDonald 1985). The series of repeated exposures to samples of an unfamiliar group were performed after the set of experiments investigating neighbour recognition had been completed.

(b) Statistical analyses

The number of worry calls and counter-marks observed during the control condition (prior to each trial) was deducted from the experimental condition. To avoid pseudoreplication, responses to the two neighbouring groups were averaged for the different locations. If the comparison of responses to stimuli of the three donor categories ('own', 'neighbour' and 'stranger') was significant, we conducted a planned post hoc comparison of responses to stimuli of neighbouring groups and strangers.

Group-level responses to scent-mark translocation experiments (number of individuals giving worry calls, number of individuals counter-marking and number of inspections) were normalized by square-root transformation and analysed in linear mixed

models (LMM) using the restricted maximum likelihood method and type I sums of squares. Since group size changed markedly throughout the study period for some groups, group size of the experimental group (number of adults) was included as a covariate in the initial model, but dropped if the p-values for the main effect and all interactions were larger than 0.1. Group identity was included as a random factor but dropped if redundant (variance component less than 10^{-5}). In the latter case, a linear model (LM) was calculated.

On the individual level, we analysed the duration of single inspection bouts (log-transformed) in a LMM, additionally controlling for sex of the inspecting individual, sex and age of the animal that had contributed the sample, sample type and inspection order (first, second, ... sample a particular individual inspected). Identity of the inspecting individual (nested within group) was included as an additional random factor. For the latter analysis, we used only bouts with known identity of the inspecting animal and with bout length determined to the nearest 2 frames (0.16 s), in total 3133 bouts of 142 individuals in seven groups and ten trials per group.

For the series of exposures to scent marks of an unfamiliar group, three response variables were analysed on group level: number of worry calls emitted; number of counter-marks (both square-root transformed); and total duration of interest measured as the amount of time for which at least one individual was inspecting the presented excreta. Since group sizes changed by no more than one individual throughout these series, we analysed these data using repeated measures ANOVA. Data analysis was carried out in R v. 2.2.1 (R Development Core Team 2005).

3. RESULTS

(a) Life history

During the course of this study, 233 animals were born and 211 animals died or disappeared. Twelve of 51 animals, for which the cause of mortality was known, were killed by neighbouring groups (eight infants and four adults). The size of some groups changed considerably between years due to death and recruitment of offspring. Of the seven groups studied, two increased in size (group size in March 2004, 11 and 18,

respectively; in March 2005, 19 and 29, respectively), one decreased (34 to 23 individuals) and four remained largely constant. The two groups increasing in size expanded their home ranges considerably at the expense of neighbouring groups (see electronic supplementary material).

Seventy-three aggressive interactions between neighbouring groups were observed during the course of the study (0.02 interactions per observation hour). At least 22 of these interactions included serious aggression (body contact). Floaters were seen near the studied groups on 13 occasions, but no serious aggression towards them was observed.

(b) Neighbour-stranger discrimination

For the subset of experiments for which we had recorded the means of collection, samples collected ad libitum were neither inspected longer than samples collected by trapping (LMM with group and individual as random factors and controlling for significant effects of sample type, sample age and inspection order; $F_{1,672}$=0.70, p=0.40) nor did groups inspect them more often (LMM with group as random factor and controlling for significant effects of sample type, location of the experiment and donor category; $F_{1,57}$=0.001, p=0.98; 'trapped' samples: N=8, 'ad libitum' samples: N=62).

Presenting excreta of neighbours or strangers elicited worry calls in 80% of all experiments. Worry calls never occurred during the control condition, when herbivore faeces and water were presented. Only in one out of twelve experiments was a worry call given in response to samples of the own group. The number of individuals giving worry calls differed among the three donor categories (LMM, $F_{2,27}$=26.3, p<0.001; figure 1*a*) and was twice as high for the neighbour treatments as for the stranger treatments ($F_{1,18}$=9.27, p=0.007). The response did not differ between locations of the presentation (centre versus border; $F_{1,18}$=1.09, p=0.31). In response to two out of the four neighbour treatments, one group emitted acoustically different calls typically given during agonistic group interactions ('war cries') in addition to worry calls (for spectrograms see electronic supplementary material).

In 75% of all experiments, the presented scent marks evoked counter-marking. In 10% of the experiments, scent marking was also observed during the control condition. Taking this into account, the number of adults counter-marking neither differed among

treatments (LMM, $F_{2,27}$=0.59, p=0.56; figure 1*b*) nor between locations ($F_{1,27}$=0.97, p=0.33), nor was there an interaction between the two factors ($F_{2,27}$=0.44, p=0.65).

The number of inspection bouts differed among the three donor categories (LMM, $F_{2,27}$=9.39, p<0.001). The number of bouts was higher during the neighbour treatments than the stranger treatments ($F_{1,17}$=9.04, p=0.008) and higher at the border of the home ranges than in the centre ($F_{1,17}$=6.16, p=0.024). The duration of single inspection bouts also differed among treatments (LMM after controlling for significant effects of sex of the inspecting individual, sex and age of the animal that had contributed the sample, sample type and inspection order; $F_{2,2437}$=9.31, p<0.001; figure 1*c*). When comparing inspection bouts between 'neighbour' and 'stranger' treatments, we found no treatment effect but a significant interaction between treatment and location of the experiment ($F_{1,2108}$=30.4, p<0.001; figure 1*c*). Inspection bouts to samples of neighbours were longer in the home range centre than at the border. In contrast, inspection bouts to samples of strangers were longer at the border than in the centre of the home range.

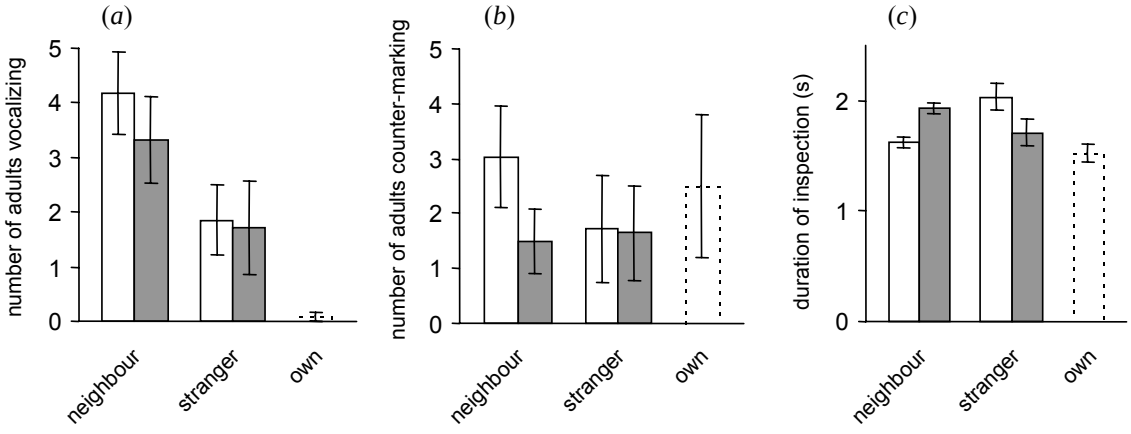

Figure 1. Responses of seven banded mongoose groups to excreta of neighbouring groups and strangers. Mean±s.e. are shown. Open bars, at the border of the experimental group's home range. Filled bars, in the centre of the experimental group's home range. Responses to scent marks of the group itself are shown on the far right in each panel. (*a*) Number of adults emitting worry calls. (*b*) Number of adults counter-marking. (*c*) Duration of single inspection bouts.

(c) Neighbour-neighbour discrimination

When presented with samples of a neighbouring group at the opposite border, fewer individuals gave worry calls than when samples of the same group were presented at the shared border (LM, $F_{1,11}$=5.11, p=0.045; figure 2*a*). The number of individuals counter-marking did not differ between shared and opposite border (LMM, $F_{1,5}$=0.14, p=0.73), nor did the number of inspections (LMM, $F_{1,4}$=0.16, p=0.71). However, single inspection bouts were longer at the opposite border than at the shared border (LMM, $F_{1,1710}$=34.2, p<0.001; figure 2*b*).

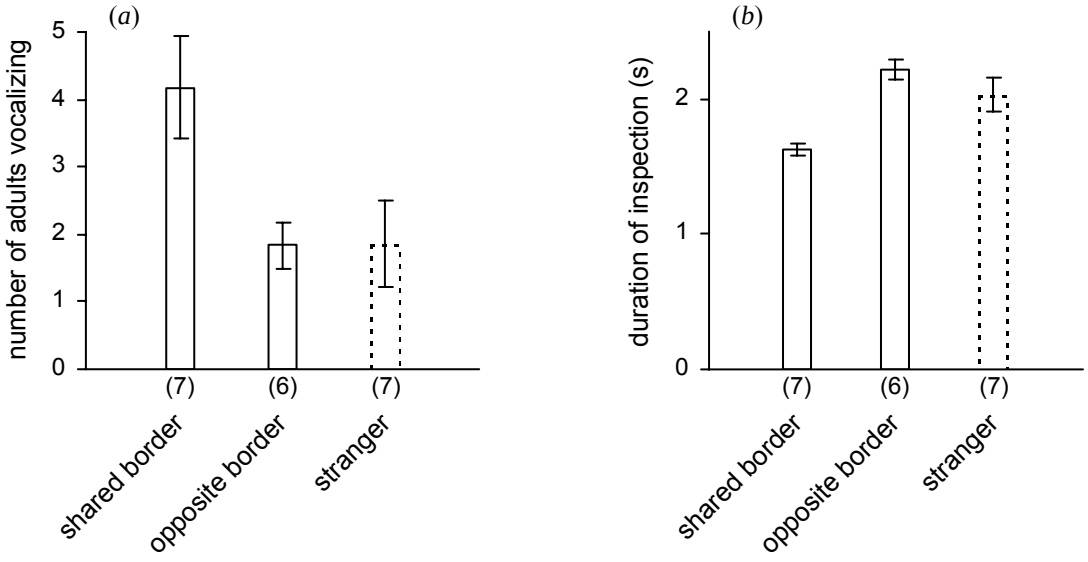

Figure 2. Responses of banded mongoose groups to excreta of neighbouring groups at the shared and opposite borders of the experimental group's home range. Mean±s.e. are shown. Reactions to excreta of strangers at the border of the home range are given for reference. Numbers in brackets give sample sizes. (*a*) Number of individuals emitting worry calls. (*b*) Duration of single inspection bouts.

When categorizing each neighbouring group used in the experiments as either larger (N=13) or smaller (N=12) than the resident group, we found no effect of relative group size on the number of individuals emitting worry calls (LM correcting for location of the experiment, $F_{1,22}$=1.45, p=0.24), on the number of individuals counter marking (LMM, $F_{1,16}$=0.08, p=0.78) or on the number of inspection bouts (LMM, $F_{1,16}$=0.31, p=0.58). However, single inspection bouts were longer when samples of a smaller rather

than a larger neighbouring group where inspected (LMM, $F_{1,1710}$=6.26, p=0.012). This effect was restricted to urine samples and did not occur for faeces (sample type×donor size interaction, $F_{1,1710}$=13.8, p<0.001).

(d) Repeated exposure to scent marks of strangers

The intensity of the response to repeated presentation of scent marks from strangers declined over time (figure 3). During the later trials, fewer worry calls were emitted (repeated measures ANOVA, $F_{3,15}$=9.84, p=0.0008) and the duration of interest was reduced ($F_{3,15}$=4.79, p=0.016). The number of counter-marks tended to be lower during the later trials ($F_{3,15}$=2.46, p=0.10).

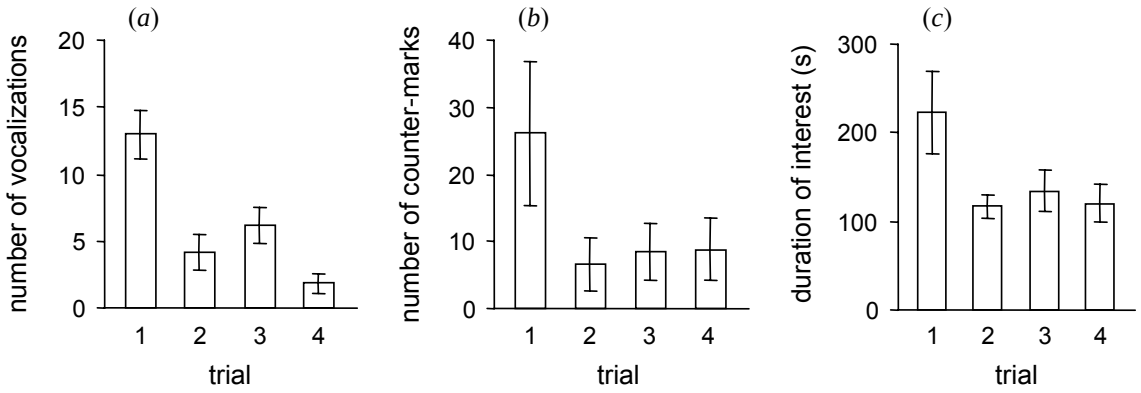

Figure 3. Reactions of six banded mongoose groups to repeated exposure to excreta of strangers. Mean±s.e. are shown. (*a*) Number of worry calls. (*b*) Number of counter-marks. (*c*) Duration of interest measured as amount of time for which at least one individual was inspecting the presented excreta.

4. DISCUSSION

We tested two hypotheses that attempt to explain relationships between territorial neighbours, and in particular, the wide occurrence of NSD throughout the animal kingdom. The familiarity hypothesis and the threat-level hypothesis (Temeles 1994) make contrasting predictions when neighbours represent a higher threat to residents than

strangers. This situation might be common in social species, in which large stable groups defend territories, such as in the banded mongoose.

Adult banded mongooses discriminated between neighbours and strangers. More animals emitted worry calls and individuals performed more inspection bouts in response to scent marks of neighbouring groups than to scent marks of strangers. We interpret worry calls, which recruited other group members to the site, as a correlate of response intensity. Inspection of the scent marks from neighbours may be increased because individuals gather information about dispersal opportunities as well as age, health and reproductive status of members of the neighbouring groups. The same information about strangers may also be relevant, but less so, since they likely represent transient animals that may not be encountered again. The number of animals counter-marking did not differ between 'neighbour', 'stranger' and 'own group' treatments. This suggests that counter-marking is not exclusively used for territory defence, but may serve other purposes within the group such as group cohesion or mate guarding (Jordan et al. in press).

As predicted by the threat-level hypothesis, neighbours elicited a stronger response than strangers. In banded mongooses, neighbours pose a considerable threat as potential usurpers of territories, opponents in lethal fights and competitors for mates (Cant et al. 2002). Strangers, in contrast, commonly represent small, single-sex dispersing splinters that are typically outnumbered by their same-sexed rivals in established groups (Cant et al. 2001; Banded Mongoose Project 2005, unpublished data) and, thus pose little threat. The stronger response to scent marks of neighbours than to samples of strangers cannot be explained by habituation. Neighbouring groups meet regularly (Cant et al. 2002; Gilchrist & Otali 2002) and encounters with scent marks of neighbouring groups at the territory border occur on a daily to weekly basis (C. A. Müller 2005, personal observation). The familiarity hypothesis, thus, predicts a reduced response to the stimuli of neighbouring groups, which is the opposite of what we found. Even so, repeated exposure to scent marks of the same unfamiliar group, simulating a new group settling nearby, led to weaker responses over time. Thus, even though mongooses habituate to olfactory stimuli from foreign groups, the response to scent marks of neighbours is increased. This suggests that, only after physical encounters have taken place, are neighbouring groups treated as a larger threat than strangers. These encounters may be seen as invasion attempts and, thus, as indication that the neighbouring group cannot be trusted (Godard 1993; Olendorf et al. 2004). Since all groups regularly engaged in fights

with all of their neighbours, 'trustworthy' neighbours, which could be expected to be treated like dear enemies, did not occur in our study population.

Only few studies to date have investigated responses to neighbours and strangers in social vertebrates. Recently, a stronger response to stimuli of neighbours than of strangers has been shown in another social mammal with intense competition between neighbouring groups, the chimpanzee (*Pan troglodytes verus*; Herbinger 2004). In contrast, green woodhoopoe (*Phoeniculus purpureus*) groups respond less intensely to neighbours than to strangers (Radford 2005). However, in green woodhoopoes, group sizes are considerably smaller (2-9, mean=3, N=31, not including dependent young; Radford & Du Plessis 2004) than in the chimpanzees studied by Herbinger (10-52, mean=28, N=3; Herbinger 2004) or in banded mongooses (5-60, mean=24, N=9, present study). Thus, a numerical disparity between neighbouring groups and strangers is probably reduced or absent in woodhoopoes. Furthermore, when woodhoopoe groups are defeated in territorial disputes with neighbouring groups, they lose little, since victorious neighbours only briefly intrude into the defeated group's territory and no permanent changes in the territory boundaries are observed. However, woodhoopoe groups may lose their territory to strangers (Radford 2005). The weaker response to neighbours than to strangers observed in woodhoopoes is thus in accordance with both the familiarity and the threat-level hypotheses.

The duration of inspection bouts in banded mongooses was influenced by the source of the samples as well as by their spatial occurrence. Excreta of neighbours were inspected longer when encountered in the centre of the focal group's home range than when encountered at the border. In contrast, samples of strangers were inspected longer when encountered at the border than in the centre. Samples from strangers encountered at the border may represent a new group settling nearby or a recent takeover in a neighbouring group. Thus, it may pay to gather additional information about these potential new neighbours. Conversely, samples from strangers encountered in the centre of a group's home range are probably from transients, which are less likely to be encountered again. The pattern found for neighbours may be explained by increased inspection when excreta are encountered out of the usual (spatial) context, which may represent an attempt of a neighbouring group to expand its territory. The duration of inspection bouts during the 'neighbour' treatments increased from shared border to centre to opposite border of the focal group's home range (figures 1*c* and 2*b*).

The threat-level hypothesis not only predicts a stronger response to neighbours than to strangers in banded mongooses, but also a stronger response to larger compared to smaller neighbours. However, we found that the response to larger neighbouring groups was not stronger than to smaller ones. This indicates that banded mongooses distinguish between different threat levels only in a crude way (even smaller neighbouring groups are typically still considerably larger than dispersal splinters representing strangers). Alternatively, mongoose groups may be unable to monitor the size of their neighbours. We believe this is unlikely since fights between groups are decided by group size (Cant et al. 2002) and, thus, groups remembering the outcome of recent fights also know if the respective neighbouring group is larger or smaller than themselves. Furthermore, we found that mongooses inspected urine samples of smaller neighbouring groups longer than urine of larger ones. This may reflect that smaller neighbours more likely offer an opportunity to disperse and take over. It also indicates that mongooses are able to distinguish larger from smaller neighbouring groups.

Although adult banded mongooses did not discriminate between neighbouring groups according to relative group size, they nevertheless discriminated between different neighbours. Excreta were inspected longer and elicited fewer worry calls when presented at the opposite border than when presented at the shared border. The response to neighbours at the opposite border was not different from the response to strangers (figure 2). These results suggest that stimuli of neighbours, when encountered at the 'wrong' border, are considered to represent dispersing animals and are therefore treated like stimuli of strangers, even though neighbours are probably still recognized when encountered in a novel location (as in frogs, Bee & Gerhardt 2002). Presence of NSD at the shared border and absence at the opposite border has also been found for species exhibiting a 'dear enemy effect' (e.g. Stoddard et al. 1991; Radford 2005). Therefore, stimuli of familiar conspecifics encountered in a novel location do not automatically lead to a stronger response, but may lead to a weaker response (in this case fewer worry calls). The latter finding cannot be explained by dishabituation.

Our findings support the hypothesis that NSD in banded mongooses is based on varying threat levels represented by neighbours and strangers. For this species, we can reject the hypothesis that neighbours and strangers get treated differently because residents are more familiar with neighbours than with strangers. However, banded mongooses may respond to different threat levels in a crude way without discriminating further between larger and smaller neighbouring groups. We suggest that 'nasty

neighbours' instead of 'dear enemies' are commonly found in social species with intense competition between neighbours and with large numerical differences between groups of neighbours and strangers. We believe that studies of taxa with differences in their social system, as well as studies of species in different contexts (e.g. breeding versus non-breeding, Leiser 2003; more or less attractive/aggressive neighbours, Olendorf et al. 2004; Hyman & Hughes 2006) will help to elucidate the causes of the taxonomically widespread phenomenon of neighbour recognition and promote understanding of the relationships between territorial competitors.

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ELECTRONIC SUPPLEMENTARY MATERIAL

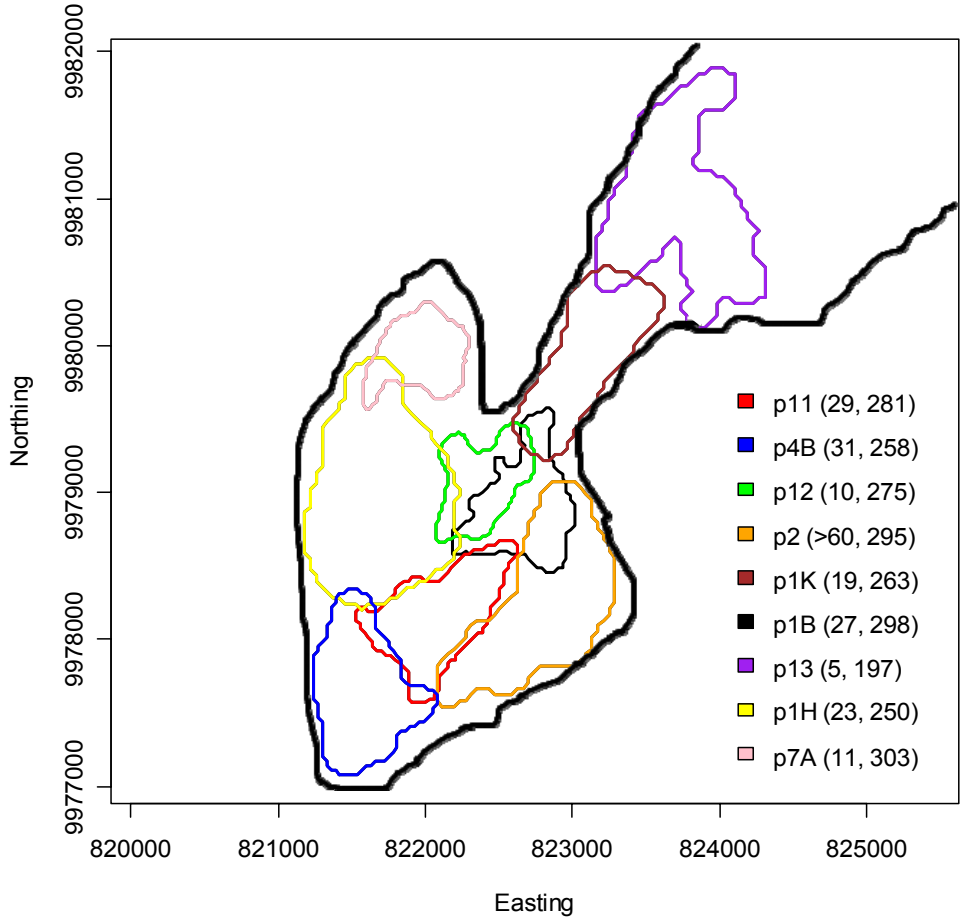

Figure S1. Home ranges of nine banded mongoose groups (p11, …) between March 2004 and September 2005 given as 90% isopleths (contour lines of equal utilisation density) of Epanechnikov kernels (Epanechnikov 1969) calculated using the 'adehabitat' package (Calenge 2006). The contour of Mweya Peninsular is given as a bold black line. Numbers in brackets give group sizes as of March 2005 and number of GPS-recorded locations. Two poorly habituated groups were not included in the experiments (p2 and p13).

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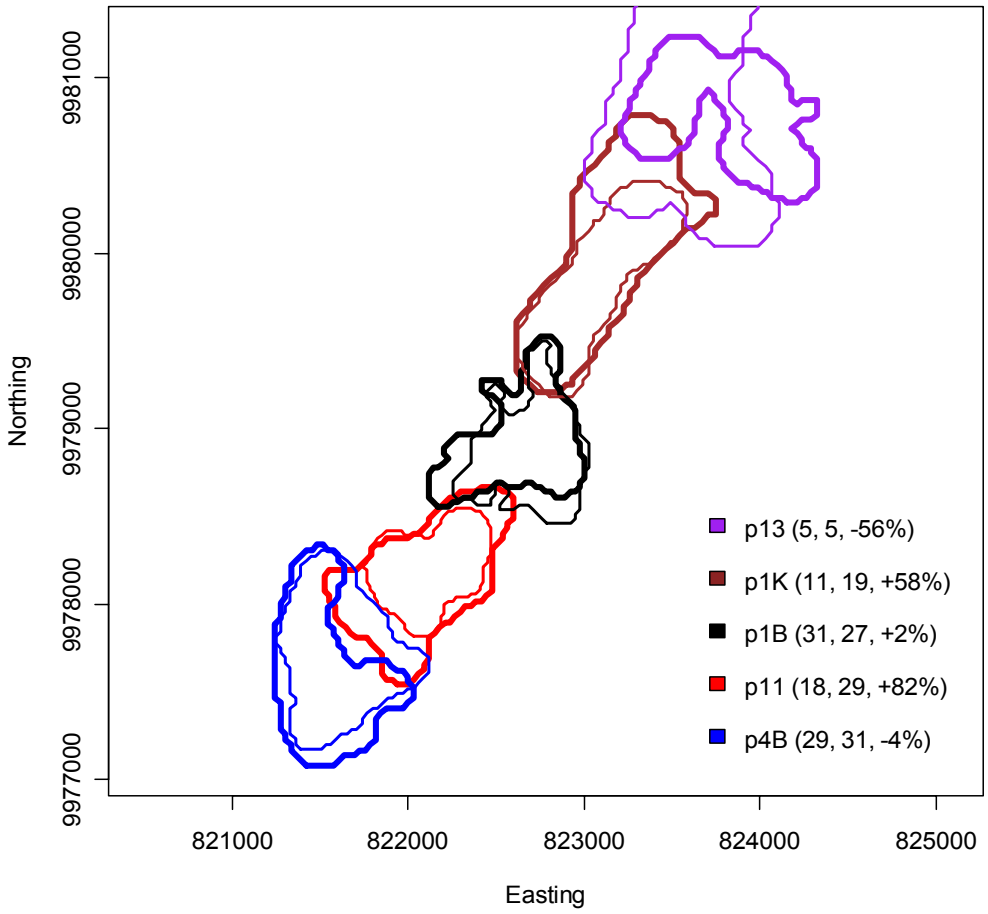

Figure S2. Changes in home range size between 2004 and 2005 for some of the studied groups. For clarity, only groups that expanded their home range considerably and group at whose expense these expansions took place are shown. Colour codes for groups are as in figure S1. P11 (red) and p1K (brown) increased in size considerably from 2004 to 2005 and expanded their home ranges at the expense of neighbouring groups (p4B, p1B and p13 respectively). Home ranges are given as 90% isopleths of Epanechnikov kernels. Thin lines: home ranges between April and September 2004. Thick lines: home ranges for the same period in 2005. Numbers in brackets give group sizes as of March 2004, group sizes as of March 2005, and changes of home range size ([size2005-size2004]/size2004). P13 lost a large part of its home range in the North to an un-habituated pack and ceased to exist by August 2005. Number of recorded GPS-locations are for p11: 202 (2004), 201 (2005); p1K: 188, 192; p13: 74, 78; p1B: 167, 164; and p4B: 134, 165.

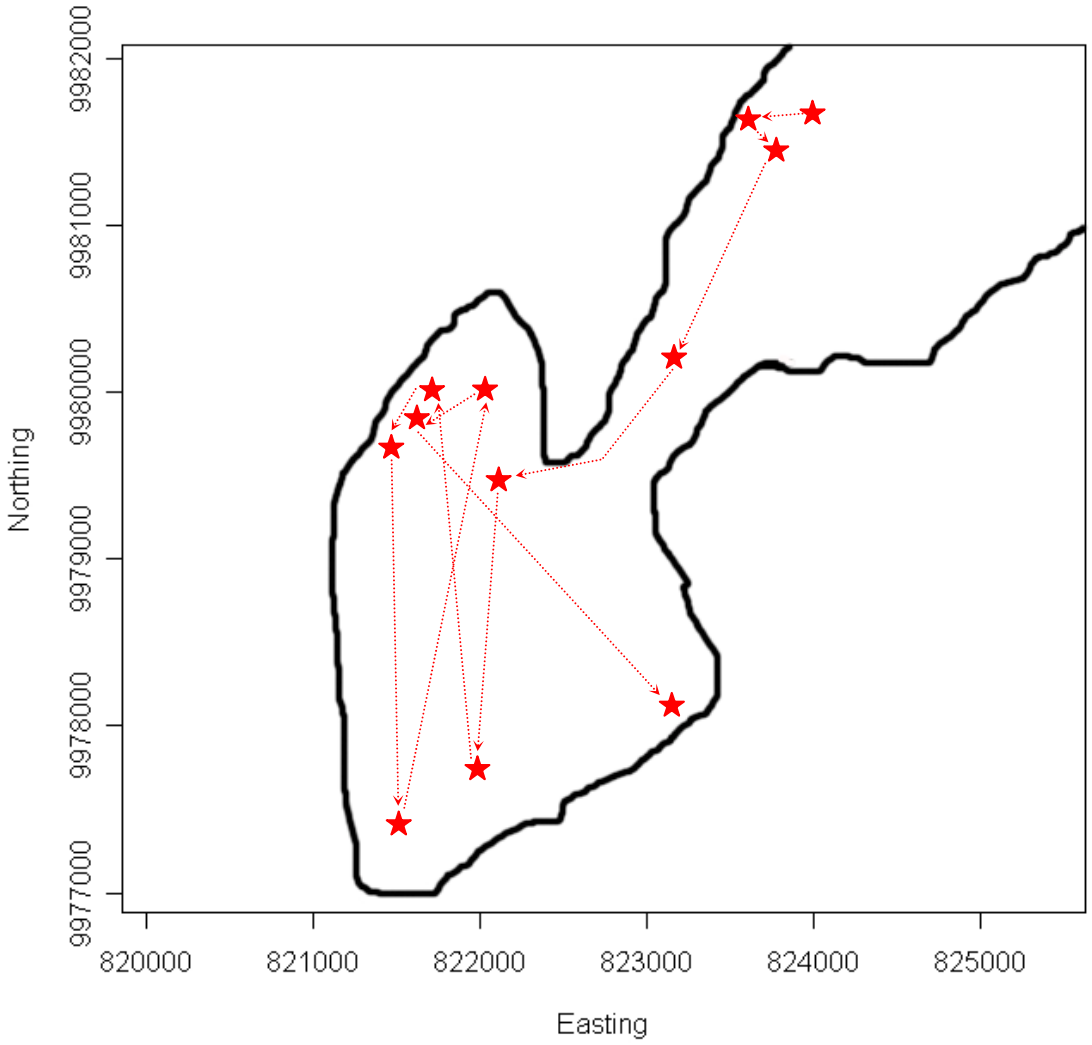

Figure S3. Sightings of an individually marked male floater, which was evicted from his group in June 2004. Arrows connect sightings between August 2004 and September 2005 in chronological order.

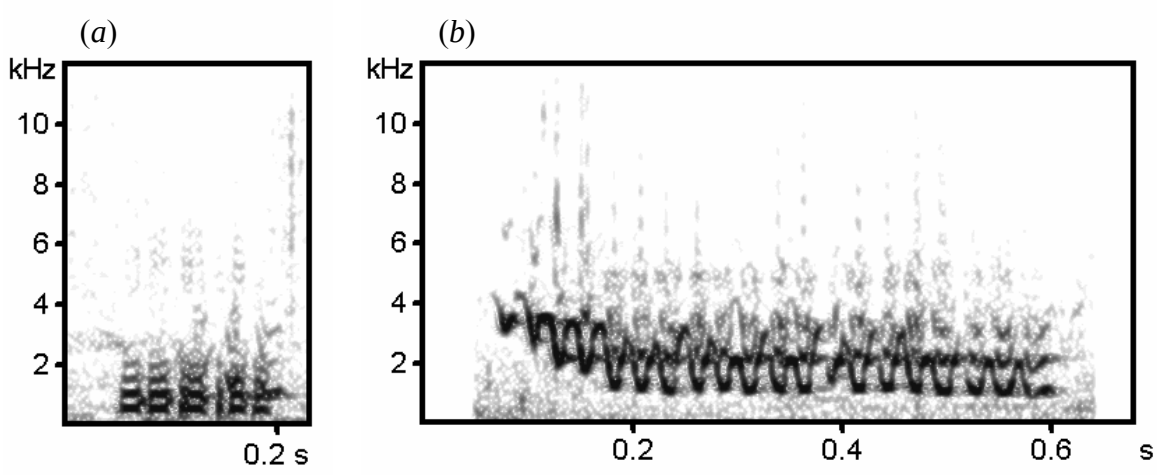

Figure S4. (*a*) Spectrogram of a typical worry call given by banded mongooses when inspecting excreta of a foreign group. For recruitment effect see supplementary video. (*b*) Spectrogram of an agonistic group-interaction call ('war cry').

APPENDIX

Playbacks of contact calls from the own group, neighbours and stranger

Summary

Since banded mongooses use a variety of vocalizations during group encounters, we also used playback experiments to test for neighbour-stranger discrimination. We used contact calls (calls that are constantly emitted by all group members during foraging) for these experiments because these calls are used for individual recognition within groups and because they are comparably easy to obtain (see Chapter 3).

The banded mongooses did not respond differently to playbacks of contact calls of neighbours and strangers. Three explanations for this finding are likely. Banded mongooses may rely on olfaction as their primary sensory modality for communication between groups and for the task of discriminating between neighbours and strangers. This is not surprising as territory borders are advertised using scent marks (pers.obs.). Conversely, unlike some other carnivores, banded mongooses do not use long-range vocalizations for territory defence. We cannot rule out, however, that banded mongooses discriminate between neighbours and strangers on the basis of other calls, such as lead calls or agonistic group interaction calls, which occur more commonly than contact calls when groups meet. Alternatively, the failure to show a discriminatory response to the playbacks may be due to two weaknesses in the experimental design: We had only six groups available which were habituated to a level that allowed conducting these experiments. Low statistical power may thus be an issue. However, we found consistent differences in the response to playbacks of the own group's calls and to playbacks of calls of strangers even with this small sample size. Furthermore, banded mongooses approached the speakers very closely when contact calls are played back, actively searching for the animals presumed vocalizing. The lacking discrimination between calls of neighbours and strangers may be because the mongooses failed to find the vocalizing animals and, consequently, ignored the stimulus.

Methods

Each group was exposed to three playbacks of contact calls in separate trials: calls of a neighbouring group, calls of strangers, and, for reference, calls of the group itself. Experiments with the same subject group were randomized in order and spaced apart by at least 7 days. Playbacks consisted of 15 contact calls of three adult individuals (one male and two females or vice versa). All calls had been recorded no longer than 4 months before being used in an experiment, using a Marantz PMD670 audio recorder and a Sennheiser ME 66/K6 directional microphone. Each individual contributed five calls to the playback. The amplitudes of all calls were standardized in CoolEdit 2000 (Syntrillium Software Corporation, Scottsdale, AZ, USA). The order of calls was randomized and inter-call intervals were randomly varied between 0.5 s and 3.5 s simulating the natural situation. Playbacks were done using the Marantz recorder and commercially available speakers (CREATIVE No-CSW5300). Calls were played back in a loop for three minutes at 30 calls per minute. Playback volume was set to 42 dB (40-45 dB) at 50 cm using a Voltcraft 329 soundlevel meter. This is marginally above the naturally observed amplitude of contact calls in banded mongooses. For each trial the speakers were placed in front of the subject group (in travel direction) 8-12 m from the nearest individual. Playbacks were only conducted if at least half of the group had been foraging uninterruptedly during the preceding half hour.

Response latency (from start of playback until the first individual approached the speakers to within 1 m) and response duration (from first approach until the last individual left the speakers) were measured, and any vocalizations given during the playbacks were recorded. Additionally, the change of group behaviour was estimated for five groups (one group did not allow following at close distance). For 10 minutes before start and after end of the playback, the group's behaviour was recorded as foraging, resting, moving, and other behaviours, assigning four points every minute. For instance, three points for foraging and one point for resting means that during that minute three quarters of the group were predominantly foraging and one quarter was predominantly resting. Values were summed for each behaviour category separately. The absolute differences (before minus after playback) were summed over all four behaviour categories to attain an index of behaviour change. Change of travel speed and travel direction were determined from GPS readings taken at the barycentre of the group every minute for 10 min before and after the playbacks.

Results

Banded mongoose groups did not discriminate between vocal stimuli of neighbouring groups and strangers. Response latency and response duration did not differ between the two treatments (paired t test; latency: t_5=2.23, p=0.08; duration: t_5=-0.27, p=0.80), and neither did groups change their behaviour, travel direction, or travel speed more after the neighbour treatment than after the stranger treatment (all p>0.30). However, all tested groups responded with shorter latency to and changed their behaviour more after the stranger treatment than after the playback of the own group's calls. Vocalizations of members of the subject groups occurred too seldom to allow statistical evaluation. During three trials (two neighbour trials and one stranger trial), lead calls were given during the playbacks. Worry calls and agonistic group-interaction calls (as observed during the scent-mark translocation experiments) never occurred during the playback experiments.

CHAPTER 2

Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew

Submitted to Ethology

Scent-marking and intrasexual competition in a cooperative carnivore with low reproductive skew

Corsin A. Müller & Marta B. Manser

Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

ABSTRACT

Most mammals scent-mark and a variety of hypotheses have been put forward to explain this behaviour. Differences in the main function of scent-marking between species are likely to be related to differences in social systems. Here, we investigate the functions of scent-marking in a cooperatively breeding carnivore. In the banded mongoose (*Mungos mungo*), individuals of both sexes commonly breed in their natal group and reproductive skew within groups is low. Using experimental scent-mark presentations, we tested predictions of the intrasexual competition, self-advertisement to potential mates and dominance assertion hypotheses. Both males and females responded more intensely to scent marks of same-sexed than of opposite-sexed individuals. Dominant individuals counter-marked more than subordinate ones and males showed higher counter-marking rates than females, but only marginally so. During oestrus, responses to scent marks were increased by both sexes. Our findings strongly indicate that scent-marking in the banded mongoose primarily serves a purpose in intrasexual competition both between and within groups. Unlike in other social herpestids and some solitary rodents, we found little evidence for self-advertisement. We suggest that the peculiar social system of the banded mongoose results in self-advertisement losing importance in this species, shifting the main function of scent-marking to intrasexual competition.

INTRODUCTION

Most mammals scent-mark, with urine, faeces and/or secretions of scent glands (Ralls 1971; Thiessen & Rice 1976). The main function of scent-marking was long thought to be territory defence (Hediger 1949; Gosling 1982; Gorman 1990). However, in a number of species the territory defence hypothesis is not supported by empirical data and some non-territorial species also scent-mark (Ralls 1971; Johnson 1973; Heymann 2006). Scent marks probably mediate individual and group recognition in most species (Ralls 1971; Johnson 1973; Gosling & Roberts 2001), whereas in only few species labelling of the home range is thought to be an important function of scent-marking (e.g. black rhinoceros: Goddard 1967; slow loris: Seitz 1969; klipspringer: Roberts 1997) and evidence is mostly indicative or the orientation hypothesis is accepted as default after rejecting other hypotheses (Brashares & Arcese 1999).

Several other, not mutually exclusive functions have been proposed, including intrasexual competition, self-advertisement to attract mates and dominance assertion (reviewed in Ralls 1971; Johnson 1973; Gosling & Roberts 2001). Support for the intrasexual competition and self-advertisement hypotheses has accumulated particularly in primates (reviewed in Heymann 2006), rodents (Rich & Hurst 1999; Thomas & Wolff 2002; Wolff et al. 2002) and herpestids (Wenhold & Rasa 1994; Jordan in press). The dominance assertion hypothesis applies in particular to social species but is difficult to disentangle from the intrasexual competition hypothesis since dominance and competition over reproduction are often tightly linked (Drews 1993; Heymann 2006).

The main function of scent-marking in a given species is probably related to its social system. In solitary species, territory defence and self-advertisement to attract mates may be more important than intrasexual competition for breeding opportunities. In social species, dispersal differences are probably linked to different roles of scent-marking. Individuals that leave the natal group to breed elsewhere, in mammals that is typically the males (Greenwood 1980), probably profit from self-advertisement to potential mates, but do not compete with same-sexed residents of their natal group. In contrast, philopatric individuals may have no need to attract mates but rather to secure their breeding position against same-sexed competitors. Here, we investigate the functions of scent-marking in the banded mongoose (*Mungos mungo*), a small, cooperatively breeding carnivore, which

is particularly interesting in this context because both sexes regularly breed in their natal group (Cant 1998; Gilchrist 2001) and reproductive skew is low (Cant 2000).

Banded mongooses, like other herpestids, scent-mark using faeces, urine and secretions of scent glands (Brown & MacDonald 1985; Müller & Manser 2007). In banded mongooses as well as in the closely related meerkats (*Suricata suricatta*), the spatial distribution of scent marks suggests that territory defence is not the primary function of this behaviour (Jordan et al. in press; N. R. Jordan pers. comm.). The density of scent marks is higher in the core areas of the home ranges, which matches the higher utilization of these areas. However, conspicuous marking spots shared between neighbouring groups indicate that marking may still play a role in territory demarcation. More likely, scent-marking is heavily involved in communication within and between groups. Banded mongooses not only recognize scent marks of their own group, but also differentiate between scent marks of different neighbouring groups and strangers (Müller & Manser 2007). Additionally, due to intense competition for reproduction (Cant 2000; Cant et al. 2001, 2002; Gilchrist 2006), scent-marking is probably involved in intrasexual competition and possibly in self-advertisement in this species.

Within banded mongoose groups, reproductive skew is generally low, with all mature females breeding regularly and commonly in synchrony (Cant 2000). Nevertheless, there is intense intrasexual competition for breeding opportunities among females. In large groups in particular, subordinate females may get temporarily or permanently evicted from the natal group during oestrus or pregnancy and thus prevented from breeding or forced to abort (Cant et al. 2001; Gilchrist 2006). Only a small proportion of all breeding attempts involve eviction (Gilchrist 2006) and the factors triggering an eviction event are still largely unknown. Competition among females is likely not for access to males but rather for helpers which, in this cooperatively breeding species, are crucial for the successful rearing of offspring (Cant 2003; Gilchrist 2004; Hodge 2005).

Males also compete for breeding opportunities. During oestrus, females are mate guarded by dominant males, which restricts breeding opportunities of subordinate males (Cant 2000). Oestrus of females within groups is commonly synchronized (Cant 2000) and therefore any single male can only guard one to two females per oestrus period. Thus, multiple males are breeding. Also copulations of females with males other than the mate guarding ones occur. It is not known how efficient mate guarding in this species is in securing paternity. However, since banded mongoose groups are commonly heavily male

biased (De Luca & Ginsberg 2001) young subordinate males are probably prevented from breeding. Eviction of subordinate males also occurs, but less frequently than for females (Cant et al. 2001; Gilchrist 2001; Hodge 2003; Bell 2006).

Intrasexual competition extends beyond the own group for both sexes. Individuals of either sex may leave the natal group either voluntarily or via eviction by co-residents. These individuals either found new groups or attempt to take over small groups, thereby displacing their same-sexed rivals permanently (Cant et al. 2001; Gilchrist 2001). Females in oestrus may also mate with males of other groups during inter-group interactions and it has been suggested that dominant females, when in oestrus, may actively seek interactions and matings with males of neighbouring groups (Cant et al. 2002). However, contrary to meerkats (Young et al. 2005), banded mongooses of neither sex leave the group temporarily to search for mating opportunities with partners in other groups.

We used a large dataset of experimental scent-mark presentations (Müller & Manser 2007) to test predictions of the intrasexual competition, self-advertisement to mates and dominance assertion hypotheses. The intrasexual competition hypothesis predicts higher rates of scent-marking in the sex with stronger intrasexual competition. As typical for mammals, competition among males is intense in banded mongooses. However, since females also compete for breeding opportunities, sex differences in marking rates are predicted to be small. The intrasexual selection hypothesis further predicts that the response to scent marks of same-sexed individuals is stronger than to those of opposite-sexed individuals and that counter-marks are placed on top of the original marks. Furthermore, scent-marking rates should increase during oestrus. If scent-marking plays a role in self-advertisement, counter-marks should be placed separate from rather than on top of the original marks to maximize individual identity (Thomas & Wolff 2002) and females should increase their marking rate when in oestrus. Also, subordinate individuals should be particularly interested in scent marks of opposite-sexed individuals from other groups and they should increase scent-marking rates in peripheral areas compared to core areas of the groups' home ranges. Finally, the dominance assertion hypothesis predicts that scent-marking is mostly done by dominant and rarely by subordinate individuals.

METHODS

The study was conducted on a wild population of individually marked banded mongooses in Queen Elizabeth National Park, Uganda (0° 12' S, 29° 54' E) between April 2004 and August 2005 (for details on the study site see Cant 2000). The study population remained largely constant in size throughout this period and consisted of 210 to 240 individuals in nine groups, seven of which were habituated to close observation and were included in the experiments described below. The size of these seven groups ranged from 8 to 44 individuals. Animals were classified in age classes as adults (>12 months), subadults (6-12 months) and infants (<6 months). Date of birth was known for all individuals except for nine adult immigrants. All animals were trapped on a regular basis to refresh individual marks (colour-coded plastic collars or small shaves on the rump), detect pregnancies, take morphometric measures and estimate ectoparasite load (for details see Cant 2000). For trapping as well as for scent-mark presentations, small amounts of bait were used (a mix of rice and gravy).

We assigned dominance status to adult individuals based on eviction events for females and based on mate guarding behaviour for males (Cant 2000). In three of the seven groups, eviction of females was observed during the study period. This allowed a clear distinction between dominant females (aggressors) and subordinate females (evictees). In the groups where no eviction was observed, the two most senior females were considered dominant and females below 2 years of age were considered subordinate. The remaining females were not assigned to either dominance category. Males that were observed regularly mate guarding dominant females were considered dominant, whereas males were considered subordinate until they started to show mate guarding behaviour (approximately at an age of 2 years). Males that were occasionally involved in mate guarding were not assigned to either dominance category. Infants and subadults as well as adults that could not be assigned to a status category (12% of the females, 36% of the males) were not included in the analyses of dominance effects.

Scent-mark presentations

In separate trials, each group was presented with excreta collected from neighbouring groups, non-neighbouring groups ('strangers') and the group itself ('own group'). This setup allowed testing the role of scent-marking in communication both between and within groups. Treatments were performed in two categories of locations (centre and border of the home range). In total, we performed 96 experiments with seven subject groups. Five of these experiments were performed when females of the acceptor group were in oestrus (in total 14 individuals), and during five experiments samples collected from females in oestrus were presented (in total nine samples).

For each trial, six or seven samples of fresh excreta were collected from the donor group within 1 hour. The set of scent marks consisted of scat and urine samples from 5-7 individuals (4-7 adults and 0-3 subadults and infants) and included samples of adult males and adult females and of both excretion types. Only samples with known identity of the excreting animal were used. If insufficient samples were collected ad-libitum, we trapped several individuals and collected excreta from the traps. This procedure represented only minimal stress, since all individuals in the study population have been trapped on a regular basis (2-4 times a year, for details see Cant 2000). All animals were released within 15 min of trapping, which is well below the delay time between peak of hormones in the blood and in the faeces for mammals (Palme et al. 2005). However, we cannot exclude that faecal samples collected by trapping were more or less likely to include secretions from the anal glands (Asa et al. 1985). Less than 20% of all samples were collected by trapping and these were not inspected longer than samples collected ad-libitum (Müller & Manser 2007).

The collected samples were stored on ice and presented to the experimental group on the same day (on average 2 hours after collection). Since banded mongooses often use open patches for territorial marking (C. A. Müller, pers. obs.), the samples were arranged in a circle on open ground (spaced apart 30-50 cm). This enabled accurate observation of the mongooses' response from 5-10 m distance. We scattered 20-50 g of bait in a circle at 2-4 m distance to the samples to make sure that the mongooses would find the presented stimuli. The experiments were recorded for later analysis using a digital video camera (Panasonic NV-GX7) and a Sennheiser ME 66/K6 directional microphone. Recording was stopped when no individual had approached any of the presented samples for 60 s.

The following response variables were evaluated: (a) duration of inspection bouts, (b) worry calls, and (c) counter-marking. The duration of inspection bouts (one individual inspecting one sample) was determined frame-by-frame in Windows Movie Maker (1 frame = 0.08 s). Worry calls are typically given upon encountering secondary cues of other mongooses or predators and are assumed to indicate how unsettling the stimuli were to the inspecting individuals (Müller & Manser 2007). Data on different types of counter-marks were pooled (anal marking: 69% of all marks, urinating: 19%, defecating: 12%).

Statistical analyses

The duration of single inspection bouts, in total 4448 inspection bouts of 208 individuals in 7 groups, was normalized by log-transformation and analysed in linear mixed models (LMM) using the restricted maximum likelihood (REML) method and Type I sums of squares. Group identity and individual identity (nested within group) were included as random factors. All results are controlled for donor category (own group, neighbouring group, strangers) and inspection order (1st, 2nd ... sample an individual inspected during a particular experiment). All p-values reported are of the respective factor entered last in the model. Non-significant interaction terms were not included in the models. However, interaction terms that were used to test specific predictions are reported also if non-significant.

The frequencies of worry calls and counter-marks were analysed with chi-square tests comparing observed and expected frequencies which were based on the number of individuals in each class that had inspected the presented samples. For the analysis of sex-specific responses to scent marks, expected values were based on the number of male and female samples that were presented. Over all experiments, on average 4.2 male and 2.8 female samples were presented. For the analyses of subsets of the experiments, the values deviated slightly (by less than 5%). We used generalized linear mixed models (GLMMs) with the penalized quasi-likelihood method and a binary error structure to analyse which samples were more likely to elicit counter-marks and worry calls than others. For these analyses, we only used experiments during which counter-marks (or worry calls respectively) had occurred. Group identity was included as a random factor. The effect of dominance on the likelihood of scent-marking and worry calling was also analysed in GLMMs with group and individual ID as random factors. For these analyses,

we only used experiments during which both dominants and subordinates had inspected the presented samples. Data analysis was carried out in R 2.2.1 (R Development Core Team 2005).

RESULTS

Which samples elicit responses?

Inspection

The duration of inspection bouts was influenced by inspection order, donor category, sample type, sample sex, sample age category as well as sex and age category of the inspecting individual (for summary see Appendix). Samples of females were inspected longer than samples of males ($F_{1,4222}$=77.1, p<0.001), in particular by males (Fig. 1a). Samples of older individuals were inspected longer than samples of younger individuals ($F_{2,4222}$=7.0, p=0.008). This effect was restricted to adults and subadults and reversed for infants (sample age*age interaction: $F_{1,4222}$=5.38, p=0.005; Fig. 1b). Samples of dominant individuals were inspected longer than samples of subordinate individuals ($F_{1,2909}$=11.6, p=0.0007). However, samples of dominant and subordinate individuals were inspected for a different amount of time depending on donor category and sample sex (sample status*donor category*sample sex interaction: $F_{2,2909}$=8.56, p=0.0002; Fig. 2).

Worry calls

Worry calls were only given in response to samples of neighbours or strangers, but not in response to samples of the own group. Urine samples were more likely to elicit worry calls than faecal samples (GLMM, $F_{1,237}$=5.03, p=0.026; Table 1). Samples of males were as likely to elicit worry calls as samples of females ($F_{1,237}$=0.003, p=0.96) and samples of subordinate individuals were as likely to elicit worry calls as samples of dominant individuals ($F_{1,216}$=0.08, p=0.78). However, samples of subordinate males tended to elicit less worry calls (dominance*sample sex interaction: $F_{1,216}$=3.25, p=0.07).

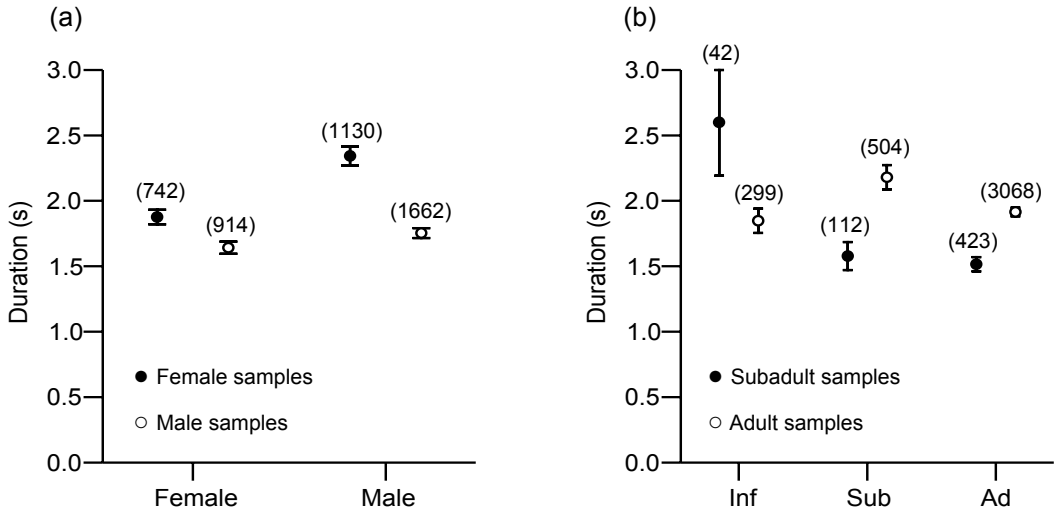

Figure 1. Duration of single inspection bouts. (a) Inspection of female and male samples by females and males. (b) Inspection of subadult and adult samples by infants (Inf), subadults (Sub) and adults (Ad). Mean ± SE are shown. Number of inspection bouts is given in brackets.

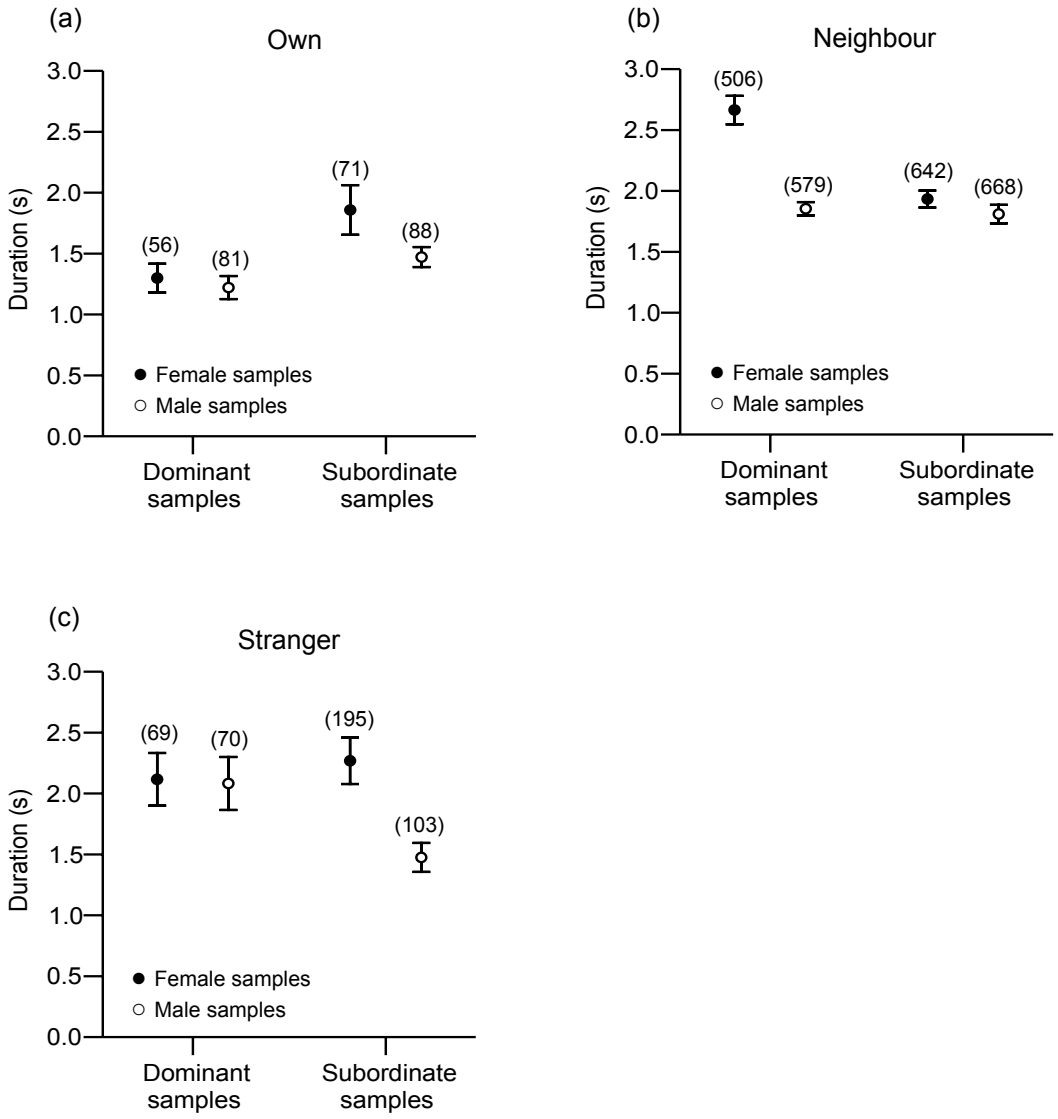

Figure 2. Inspection of samples of dominant and subordinate females and males of (a) the own group, (b) neighbouring groups and (c) strangers. Mean ± SE are shown. Number of inspection bouts is given in brackets.

Table 1. Factors affecting the probability that a sample elicited worry calls. Analysis was conducted on 266 samples presented to seven groups. Only experiments during which worry calls occurred were included in this analysis.

explanatory term	F statistic	d.f.	p
donor category (neighbour, own, stranger)	2.83	1, 237	0.09
sample sex (male, female)	0.003	1, 237	0.96
sample type (faeces, urine)	5.03	1, 237	0.026
minimal model	effect size	s.e.	
constant	-0.35	0.32	
donor category (stranger)	-0.53	0.31	
sample type (urine)	0.62	0.27	

Table 2. Factors affecting the probability that a sample was counter-marked. Analysis was conducted on 374 samples presented to seven groups. Only experiments during which counter-marks occurred were included in this analysis.

explanatory term	F statistic	d.f.	p
donor category (neighbour, own, stranger)	0.44	2, 363	0.64
sample sex (male, female)	0.25	1, 363	0.62
sample type (faeces, urine)	0.39	1, 363	0.53
minimal model	effect size	s.e.	
constant	-0.60	0.26	

Counter-marks

Urine and faecal samples were equally likely to get counter-marked (GLMM, $F_{1,363}$=0.39, p=0.53; Table 2), and so were samples of males and females ($F_{1,363}$=0.25, p=0.62). Samples of subordinates were in tendency more likely to get counter-marked than samples of dominants ($F_{1,246}$=3.47, p=0.06).

Who responds?

Inspection

Males inspected the presented samples longer than females (LMM, $F_{1,200}$=4.50, p=0.035) and were particularly interested in samples of females (Fig. 1a). Inspection effort varied among age categories ($F_{2,4222}$=4.16, p=0.016) with subadults inspecting samples longer than adults or infants (Fig. 1b). The increased inspection effort of subadults was directed equally to samples of the own and alien groups and to samples of same-sexed and opposite-sexed individuals (age*donor category*sex*sample sex interaction: $F_{1,4196}$=1.31, p=0.26; all lower interactions also not significant). Dominant and subordinate individuals spent equal time inspecting samples ($F_{1,2510}$=0.27, p=0.60). However, subordinate males were particularly interested in samples of females (sex*dominance*sample sex interaction: $F_{1,2510}$=6.02, p=0.014). This effect applied equally to samples of the own and alien groups (four-way interaction with donor category: $F_{1,2496}$=0.52, p=0.60).

Worry calls

Worry calls were given almost exclusively by adults (adults: observed 268, expected 237.4 calls; subadults: observed 7, expected 37.6 calls; $\chi^2_{(1)}$=28.8, p<0.001). Males and females were more likely to give worry calls in response to samples of same-sexed individuals than to samples of opposite-sexed individuals (males: $\chi^2_{(1)}$=4.83, p=0.028, N=148; females: $\chi^2_{(1)}$=6.71, p=0.010, N=127; Fig. 3a, b). Within adults, dominant individuals were more likely to give worry calls than subordinate ones (GLMM, $F_{1,318}$=8.29, p=0.0043), but there was no sex difference ($F_{1,108}$=1.53, p=0.22).

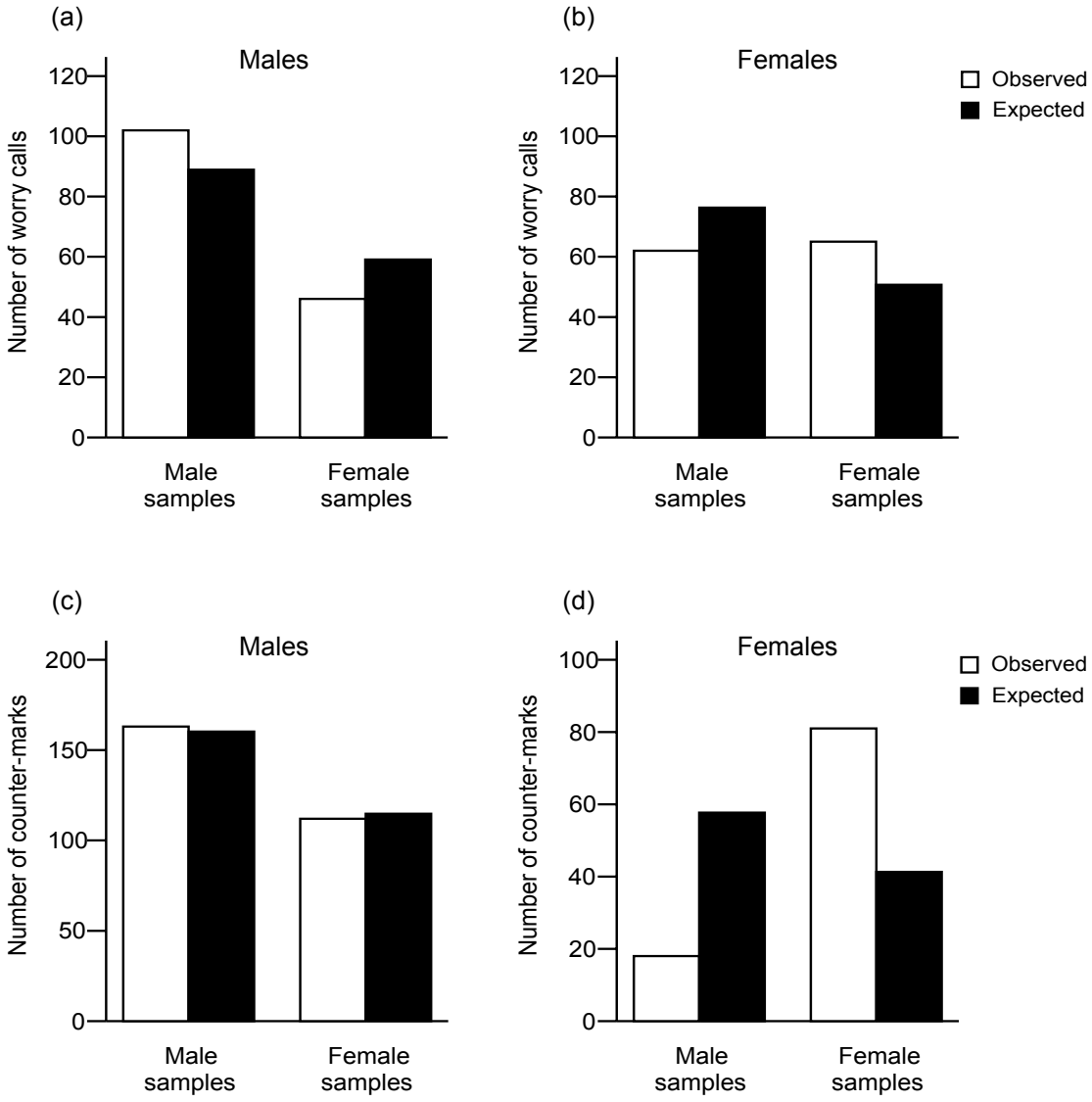

Figure 3. Observed and expected frequencies of worry calls (a, b) and counter-marks (c, d) of males and females given in response to samples of males and females. Expected frequencies are based on the number of samples of each sex presented in the experiments.

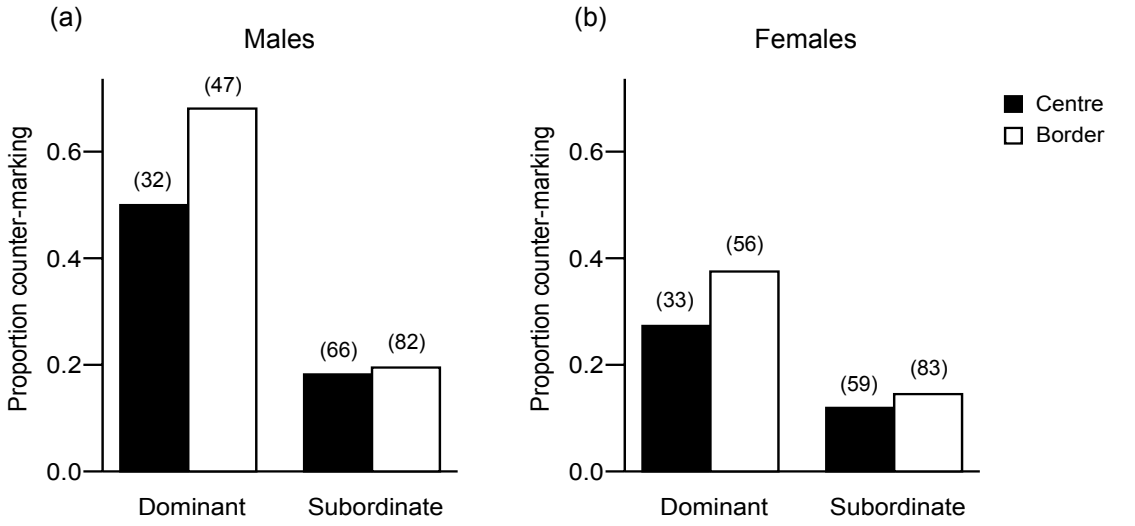

Figure 4. Proportion of dominant and subordinate individuals that counter-marked during experiments in the centre and at the border of the home range. (a) Males. (b) Females. Numbers in brackets give sample sizes.

Counter-marks

Sixty-nine percent of all counter-marks were placed on top of the original mark, 16% were placed clearly apart from the original mark and 15% were placed very close to the original mark but it could not be judged from the videotapes if the counter-mark covered the original mark or not. Counter-marks were mostly deposited by adults and rarely by subadults (adults: observed 463, expected 404.6 counter-marks; subadults: observed 16, expected 74.4 counter-marks; $\chi 2_{(1)}=54.3$, $p<0.001$). Males counter-marked more than females ($\chi 2_{(1)}=20.9$, $p<0.001$) and targeted samples of both sexes equally ($\chi 2_{(1)}=0.12$, $p=0.73$, $N=275$; Fig. 3c). Females, in contrast, counter-marked almost exclusively same-sexed samples ($\chi 2_{(1)}=65.5$, $p<0.001$, $N=99$; Fig. 3d). When analysing the response to scent marks of the own group separately, we found that both males (27 of 30 marks; $\chi 2_{(1)}=8.4$, $p=0.004$) and females (9 of 14 marks; $\chi 2_{(1)}=5.0$, $p=0.026$) preferentially counter-marked same-sexed samples. Within adults, dominant individuals were more likely to counter-mark than subordinate ones (GLMM, $F_{1,336}=31.8$, $p<0.001$). However, subordinates were still responsible for 27% of all counter-marks by adults to which a dominance status could be assigned. Subordinate and dominant individuals of

both sexes were more likely to counter-mark during experiments at the border of the home range than in the centre ($F_{1,336}$=5.22, p=0.023; Fig. 4).

Influence of oestrus on the response

Donor group in oestrus

Compared to samples of non-oestrus females, samples of females in oestrus were inspected longer (oestrus samples: $\bar{x}$ ± SE = 4.31 ± 0.53 s, N = 52 inspection bouts; non-oestrus samples: $\bar{x}$ ± SE = 2.10 ± 0.05 s, N = 1820 inspection bouts; LMM, $F_{1,1852}$=21.1, p<0.001), particularly by males (sex*sample oestrus interaction: $F_{1,1852}$=7.6, p=0.006). Compared to non-oestrus samples, oestrus samples were also more likely to get counter-marked by females (Fisher's Exact Test: p=0.022), but not by males (p=0.21).

Acceptor group in oestrus

Females in oestrus spent more time inspecting the presented samples than non-oestrus females (oestrus females: $\bar{x}$ ± SE = 2.78 ± 0.30 s, N = 89 inspection bouts; non-oestrus females: $\bar{x}$ ± SE = 1.69 ± 0.03 s, N = 1567 inspection bouts; LMM, $F_{1,1565}$=25.1, p<0.001). This increased effort was directed equally to samples of males and females (oestrus*sample sex interaction $F_{1,1565}$=0.01, p=0.94). Females in oestrus also showed a massive increase in their counter-marking rate compared to non-oestrus females (2.9 marks compared to 0.3 marks per individual and experiment, $\chi 2_{(1)}$=194.8, p<0.001) and they still targeted almost exclusively female samples (33 out of 35 counter-marks). However, this result largely depends on three females of a single group, which were responsible for 77% of the counter-marks observed during oestrus-experiments.

Males also increased their inspection effort when the females of their own group were in oestrus (oestrus: $\bar{x}$ ± SE = 2.88 ± 0.20 s, N = 240 inspection bouts; no oestrus: $\bar{x}$ ± SE = 1.91 ± 0.04 s, N = 2552 inspection bouts; LMM, $F_{1,2649}$=25.4, p < 0.001) and their increased effort was also directed equally to samples of males and females (oestrus*sample sex interaction $F_{1,2649}$=0.91, p=0.34). Males increased their counter-marking rate when the females of their own group were in oestrus (1.0 compared to 0.6 marks per individual and experiment, $\chi 2_{(1)}$=5.70, p=0.017), but much less so than the females themselves did.

DISCUSSION

We found good evidence that the main function of scent-marking in banded mongooses lies in intrasexual competition between and within groups. Both males and females counter-marked the presented samples but males did so at higher rates. The observed sex bias in counter-marking rates of 1.6 was small compared to other mammalian species, in which the scent-marking rates of males were found to be 2 to 10 times higher than the rates of females (Johnson 1973; Begg et al. 2003; Lewis 2005; Jordan in press). This may be related to considerable competition among females for breeding opportunities in banded mongooses despite comparably low levels of reproductive skew. Furthermore, adults of both sexes responded more intensely to scent marks of same-sexed than to marks of opposite-sexed individuals. In particular, both males and females were more likely to give worry calls in response to scent marks of same-sexed individuals than to marks of opposite-sexed individuals. Since worry calls were only given to samples of neighbouring groups and strangers, this reflects intrasexual competition between groups. Also, females counter-marked almost exclusively female scent marks and most counter-marks were placed on top rather than next to the original mark. Males preferentially counter-marked same-sexed scent marks when presented with samples of the own group, but counter-marked scent marks of both sexes equally when presented with samples of other groups.

Further support for the intrasexual competition hypothesis comes from the influence of oestrus on the responses to scent marks. Samples of females in oestrus were inspected longer by males and counter-marked more by females. Females in oestrus increased their inspection effort as well as their counter-marking rate. Also males increased their inspection effort and their counter-marking rate (though less markedly), when the resident females were in oestrus.

We found little evidence that scent-marking is a form of self-advertisement to potential mates in banded mongooses. First, contrary to the prediction of the self-advertisement hypothesis, most counter-marks were placed on top of the original marks rather than next to it. Second, females showed an increase in marking behaviour during oestrus as predicted by the self-advertisement hypothesis. However, males also increased their scent-marking rate when the resident females were in oestrus, which might reflect

that intrasexual competition is particularly intense during oestrus. Third, subadult individuals spent more time investigating the presented excreta than adults did. However, the increased inspection effort of subadults was found equally in response to samples of neighbours, strangers and the own group and equally to same-sexed and opposite-sexed individuals. Thus, it might reflect lack of experience rather than the checking of mating or dispersal opportunities. Finally, subordinate individuals showed slightly higher marking rates in experiments at the border of the home ranges compared to the centre. However, this increase was even more pronounced for dominant individuals. We cannot exclude that both subordinates and dominants advertise themselves to opposite-sexed individuals in neighbouring groups. Alternatively, the observed pattern might reflect that scent-marking in banded mongooses still plays a role in territory demarcation. The self-advertisement hypothesis also predicts that subordinate individuals should increase scent-marking rates during interactions with neighbouring groups. This could not be tested in the present study.

In an other herpestid, the yellow mongoose (*Cynictis penicillata*), self-advertisement was found to be a central function of scent-marking (Wenhold & Rasa 1994) and also in meerkats there is some evidence that scent-marking plays a role in self-advertisement (Jordan in press). This contrast to the banded mongoose is likely explained by differences in the social systems of these species: First, yellow mongooses of both sexes disperse from their natal group (Wenhold 1990) and also male meerkats commonly do not breed in their natal group, in which only related partners are available, but have to disperse to gain breeding opportunities (O'Riain et al. 2000). In banded mongooses, in contrast, both sexes regularly breed in their natal group and matings between close relatives are common (Cant 1998; Gilchrist 2001). Whether banded mongooses use scent-marking to advertise themselves when they have been evicted from their natal group remains to be investigated. Second, subordinate male meerkats frequently leave their group temporarily to seek matings with females of other groups (Young et al. 2005). In banded mongooses, such ‘roving’ behaviour is not observed and matings between members of different groups only occur when two groups meet and fight (Cant et al. 2002). Both factors probably contribute to subordinate yellow mongooses and meerkats having more motivation to advertise themselves to members of other groups than subordinate banded mongooses. Support for the self-advertisement hypothesis has also been found in other species in which the mating system likely makes mate attraction crucial for reproductive success, for example in promiscuous male meadow voles

(*Microtus pennsylvanicus*) and in unpaired monogamous male prairie voles (*Microtus ochrogaster*) (Thomas & Wolff 2002; Wolff et al. 2002). Also subordinate female marmosets (*Callithrix jacchus*) show evidence for self-advertisement and their potential mates are most likely encountered in neighbouring groups (Heymann 2006).

Finally, dominant banded mongooses of both sexes counter-marked more than subordinate individuals. This was predicted by the dominance assertion hypothesis but it can also be explained by intrasexual competition since our definition of dominance is tightly linked to behaviour of intrasexual competition. Moreover, a considerable proportion of subordinates (on average 16% compared to 46% of dominants, see Fig. 4) showed counter-marking during the experiments, which cannot be explained as dominance behaviour.

In conclusion, we found strong support for the hypothesis that the main function of scent-marking in banded mongooses lies in intrasexual competition both between and within groups, whereas we found little evidence for self-advertisement. Additionally, scent-marking possibly plays a role in territory defence and may be involved in dominance behaviour. However, dominance assertion is unlikely to be the main motivation for marking, since reproduction is not monopolized by a dominant pair in this species. Our findings are in agreement with a number of studies on the functions of scent-marking in social mammals (Ralls 1971; Wenhold & Rasa 1994; Heymann 2006) which found that scent-marking serves multiple purposes and that probably mate attraction and intrasexual competition rather than territory defence are the main motivation of scent-marking in these species. Our results indicate that differences in the social system, particularly in regard to natal dispersal, may shift the main function of scent-marking from self-advertisement and mate attraction to intrasexual competition.

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APPENDIX A

Factors affecting the duration of single inspection bouts. Interaction terms are given only if significant. The analysis was conducted on 4448 inspection bouts of 208 individuals in 7 groups.

explanatory term	F statistic	d.f.	p
inspection order	69.7	1, 4222	<0.0001
donor category (neighbour, own, stranger)	21.5	2, 4222	<0.0001
sample type (faeces, urine)	205.2	1, 4222	<0.0001
sample sex (male, female)	77.1	1, 4222	<0.0001
sample age category (adult, subadult)	7.01	1, 4222	0.008
sex (male, female)	4.50	1, 200	0.035
age category (adult, subadult, infant)	4.16	2, 4222	0.016
sample sex * sample type	47.5	1, 4222	<0.0001
age category * sample type	7.18	2, 4222	0.0008
age category * sample age	5.37	2, 4222	0.005
age category * inspection order	5.06	2, 4222	0.006

minimal model	effect size	s.e.
constant	1.235	0.029
inspection order	-0.013	0.0016
donor category (own)	-0.110	0.017
donor category (stranger)	-0.039	0.014
sample type (urine)	0.210	0.016
sample sex (male)	-0.029	0.013
sample age (subadult)	-0.038	0.017
sex (male)	0.037	0.017
age category (infant)	-0.173	0.037
age category (subadult)	0.069	0.030
sample sex (male) * sample type (urine)	-0.139	0.020
age category (infant) * sample type (urine)	0.141	0.037
age category (subadult) * sample type (urine)	0.019	0.029 n. s.
age category (infant) * sample age (subadult)	0.164	0.056
age category (subadult) * sample age (subadult)	-0.041	0.038 n. s.
age category (infant) * inspection order	0.030	0.012
age category (subadult) * inspection order	-0.009	0.005 n. s.

APPENDIX B

Do banded mongoose females seek extra-group matings?

Summary

Cant et al. (2002) hypothesized that females in oestrus might seek mating opportunities with extra-group males by provoking group interactions with neighbouring groups. This could be a way to avoid inbreeding since animals within groups are usually closely related. I therefore tested whether females in oestrus showed a heightened interest in scent marks of males from neighbouring males. I found little support for Cant et al.'s hypothesis. Oestrus females were more interested in samples of neighbours than of strangers as predicted by Cant et al. However, the increased inspection effort was directed to male and female samples equally. Furthermore, also the males were more interested in samples of neighbours than of strangers when the resident females were in oestrus. Thus, the pattern might reflect a generally heightened interest in scent marks of neighbouring groups during oestrus rather than seeking extra-group matings.

Results

Analysing the inspection effort of adult females and males separately, I found that, during oestrus, the females were more interested in samples of neighbouring groups than samples of strangers (LMM, source*oestrus interaction $F_{1,1421}$=12.1, p<0.001; Fig. Ia). The same pattern was found for the males when the resident females were in oestrus (source*oestrus interaction $F_{1,2374}$=12.6, p<0.001; Fig. Ib). When analysing the oestrus-experiments separately, I found that the increased interest of females in samples of neighbouring groups compared to strangers was directed equally to male and females samples (source*sample sex interaction $F_{1,145}$=0.03, p=0.87). For the males in contrast, female samples of neighbouring groups and strangers were equally interesting but male samples from neighbours were more interesting than male samples from strangers (source*sample sex interaction $F_{1,179}$=5.42, p=0.021).

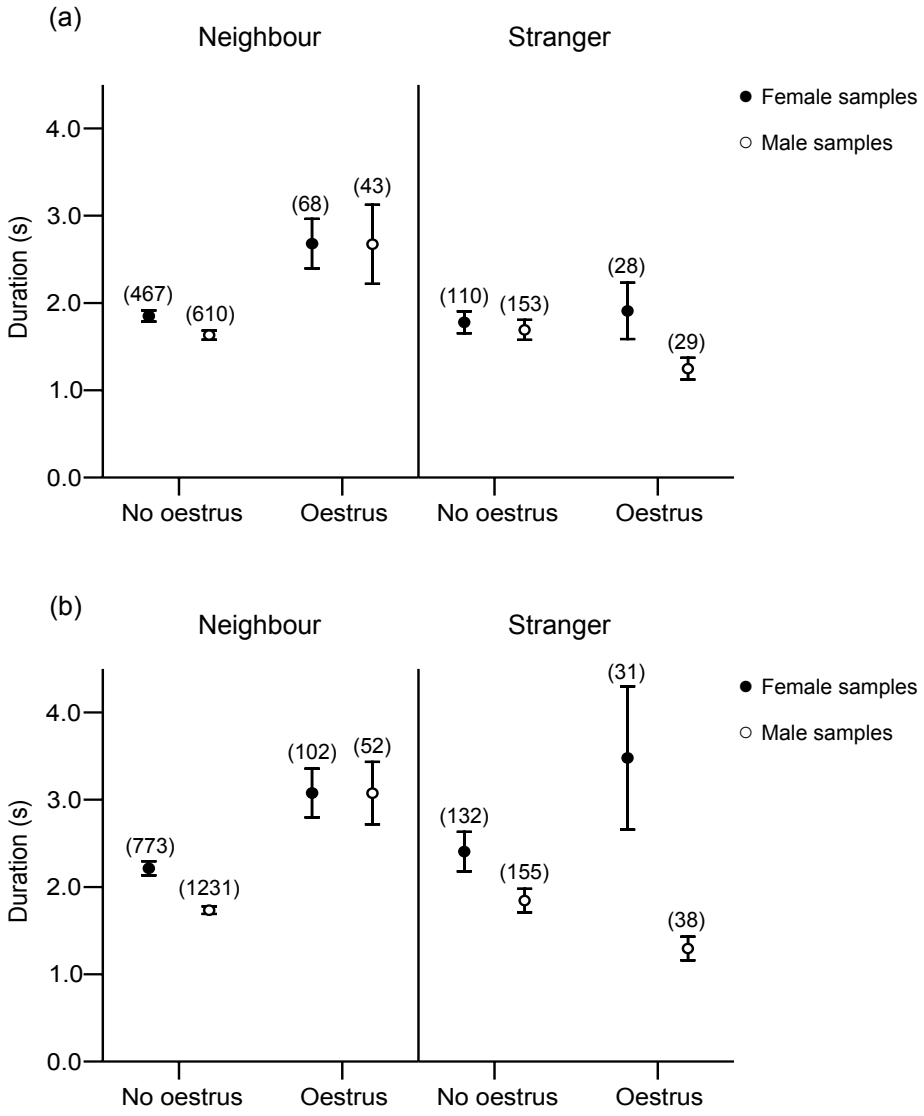

Figure I. Inspection of samples from neighbours and strangers: (a) by females in oestrus and out of oestrus, (b) by males when the resident females were in oestrus or not. Number of inspection bouts is given in brackets.

CHAPTER 3

Mutual recognition of pups and providers in the cooperatively breeding banded mongoose

To be submitted

Mutual recognition of pups and providers in the cooperatively breeding banded mongoose

Corsin A. Müller & Marta B. Manser

Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

ABSTRACT

Adults providing food to offspring are predicted to allocate care in a way that maximizes their fitness. Both parents and helpers have been demonstrated to show preferences for particular young depending on relatedness or offspring sex or size. However, little is known about how providers discriminate among individual offspring. In the banded mongoose, a cooperatively breeding carnivore with low reproductive skew, pups form long-lasting and exclusive associations with particular adults, their 'escorts', and receive the majority of care from these individuals. Here we show that pup distress calls and escort contact calls are individually distinct and, using removal experiments with subsequent playbacks, that pups and escorts recognize each other vocally and mutually. Our experiments further demonstrate that both pups and escorts are more responsive to calls of their association partners than to calls of other individuals. These results suggest that both pups and providers contribute to the maintenance of the pup-escort associations. We suggest that pups benefit from vocal recognition of their escorts since this reduces the time spent alone vulnerable to predators and without being fed. Escorts may be more responsive to their associated pup's calls than to another pup's calls because they preferentially care for this particular individual or because they were primed by constant exposure to its calls.

INTRODUCTION

Parents providing food to offspring are predicted to use a feeding regime that maximizes their long-term reproductive output (Clutton-Brock 1991). Parents may feed offspring of a brood equally (e.g. Leonard et al. 1994; Malacarne et al. 1994; Ostreiher 1997), or they may preferentially feed offspring of a particular sex, age or size (reviewed in Lessells 2002). Preferences may differ between providers when parents differ in the cost of reproduction or in the benefits they gain from different types of offspring (Lessells 2002), and in some species only one sex shows a preference (e.g. Krebs et al. 1999; Brotherton et al. 2001). In the extreme case of brood division, as observed in some bird species (reviewed in Lessells 2002), the two parents may provision separate sets of the brood almost exclusively. In a recent study on brood-dividing redstarts (*Phoenicurus ochruros*), Draganoiu et al. (2006) showed that parents discriminate acoustically between fledglings associated with them and fledglings associated with the other parent.

In a variety of bird and mammal species, non-reproductive helpers contribute to rearing offspring of other individuals, and these helpers are predicted to allocate care in a way that maximizes the benefit of helping (Brown 1987). For example, helpers may care preferentially for closely related young (Emlen & Wrege 1988; Russell & Hatchwell 2001) or increase investment when helping close kin (Reyer 1984; Komdeur 1994). Helpers may also preferentially care for future helpers, as has been suggested in meerkats where females are philopatric and females helpers contribute more to cooperative care and preferentially feed female offspring (Brotherton et al. 2001).

For both parents and helpers, the scope for favouritism is restricted by the availability of options and the ability to discriminate among offspring. Whereas most broods containing multiple offspring probably include individuals of both sexes, variation in age or size may be small, particularly in small broods, and broods of a single pair of parents may not offer variability in relatedness. Furthermore, the potential for kin recognition may be restricted if no reliable association cues are available (Komdeur et al. 2004) and preferential feeding of certain individuals requires that the offspring can be distinguished individually (Draganoiu et al. 2006).

Parent-offspring recognition in mammals is usually mediated by olfactory (e.g. Romeyer et al. 1994; Levy et al. 1996; Jackel & Trillmich 2003), vocal (e.g. Insley 2000,

2001; Searby & Jouventin 2003) or a combination of olfactory, vocal and visual cues (e.g. Keller et al. 2003). In most cases however, recognition is confounded with kinship since parents were shown to discriminate between their own and alien offspring, but not between individual offspring they were equally related to. Only few studies to date have demonstrated true individual recognition of offspring by their providers, independent of kinship or other confounding variables such as sex, age or size (e.g. Draganoiu et al. 2006). We studied individual recognition between pups and providers in a species that is particularly interesting in this regard because it offers an opportunity to test for individual recognition independent of these confounding effects.

The banded mongoose (*Mungos mungo*) is a small (< 2 kg) cooperatively breeding herpestid, in which up to 10 females of a group breed synchronously (Cant 2000) and non-reproductive individuals contribute substantially to rearing the offspring (Cant 2003; Gilchrist 2004). Banded mongooses are interesting subjects for the study of individual recognition because most pups consistently associate with the same adult or subadult 'escort'. These associations are formed in the first few days after the pups emerged from the den and commonly remain stable for the whole period of dependence (about 6-8 weeks; Gilchrist 2004; Hodge 2005). During foraging, pups spend most of the time in the immediate vicinity (< 1m) of their escorts (Gilchrist 2004; Hodge 2005). As a consequence, pups get the vast majority of food from their escorts and very little from other group members (Bell 2006). Helpers commonly feed the pup nearest to them, which is normally their associated pup, and only rarely a pup further away (Gilchrist 2004). Overall, escorts give away more food than non-escorting individuals (Gilchrist 2004). Compared to pups that do not form an escorting association (usually the smallest of a litter), escorted pups get more food, grow faster, reach age of sexual maturity earlier and have a higher survival rate (Hodge 2005). Observations suggest that these associations are formed and maintained by the pups, since the pups follow their escorts on 99% and escorts follow their pups in only 1% of all cases (Gilchrist 2004). However, experimental evidence showing which of the two parties maintains the association and how it is maintained are lacking. At short distance, pups and escorts probably recognize each other by smell. However, long distance recognition is required for the reunion after temporary separation, for example when the escort wandered off foraging while the pup was consuming a large prey item. In a habitat with a lot of structures obstructing vision (Rood 1975; Cant 2000), vocal recognition is probably the most efficient mechanism for this task.

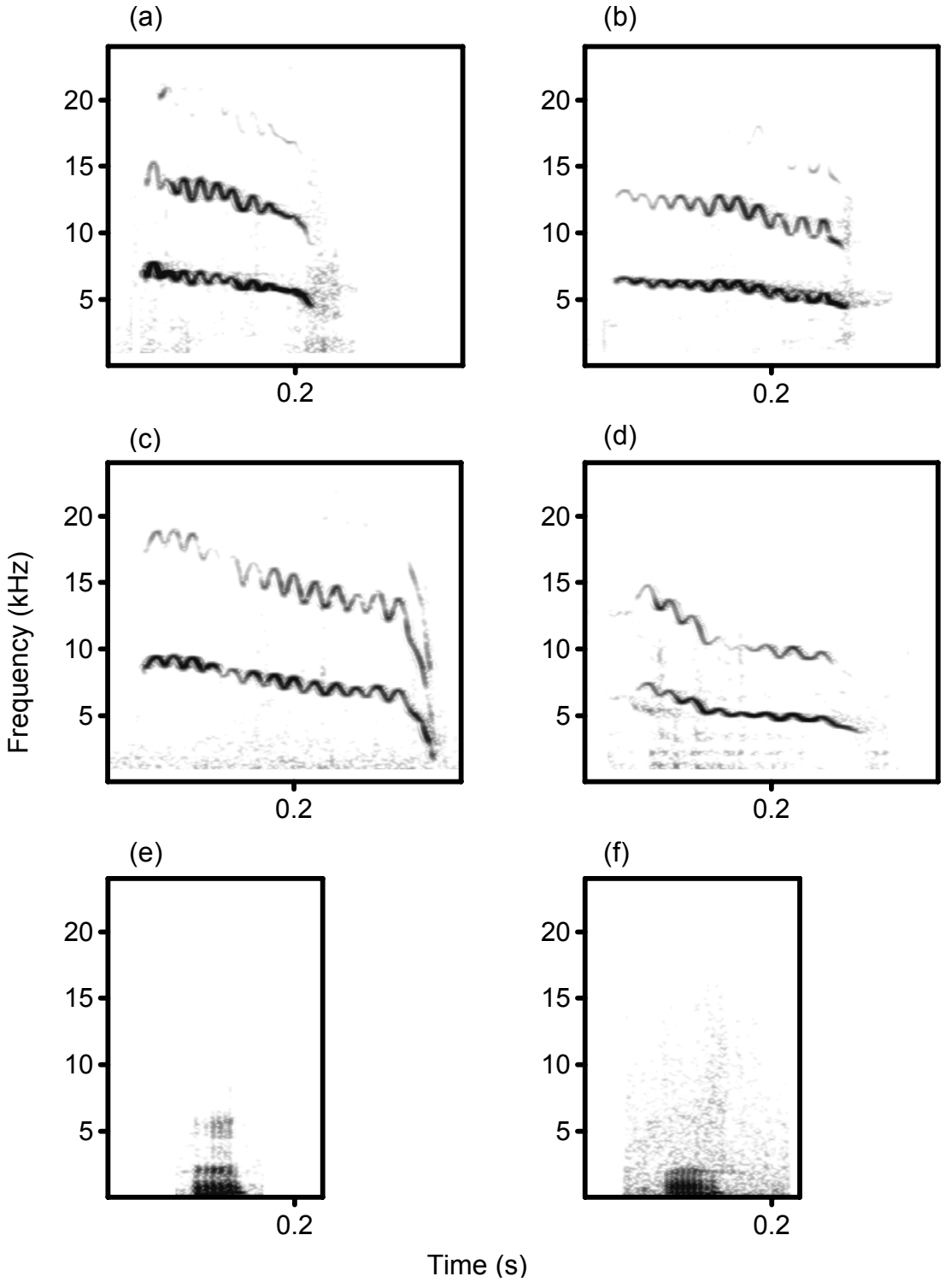

Figure 1. Spectrograms created in Avisoft (FFT length: 1024, frequency resolution: 47 Hz, time resolution: 0.67ms). (a) and (b) distress calls of two different pups. (c) and (d) begging calls of the same two pups. (e) and (f) contact calls of two different adults.

We investigated whether pups and escorts recognize the calls of their association partners and whether both parties contribute to the maintenance of the escorting associations. We first recorded pup 'distress' calls and adult 'contact' calls and analysed both call types for individual differences (for spectrograms see Fig. 1). Pups emit distress calls when they get separated from the group, but not when they are separated from their escort while they still have other group members nearby (C. A. Müller, pers. obs.). Adults constantly emit contact calls while they are foraging, both when with pups and when foraging by themselves, at a rate of 5 to 15 calls per min (C. A. Müller, pers. obs.). Since distress calls occur only rarely, we also analysed begging calls frequently given during foraging (20-60 calls per min; Bell 2006) to test whether they can serve as a template that allows individual recognition of the seldom emitted distress calls. We then temporarily removed pups and escorts in separate experiments and conducted playbacks to test whether pups recognize their escort's calls and vice versa. Additionally, these experiments allowed us to test which of the two parties contributes to the maintenance of the escorting association. Since pups clearly benefit from escorting associations, we predicted that pups would recognize their escort's contact calls and that they would preferentially respond to playbacks of these calls compared to contact calls of other adults. If escorts recognize their associated pup vocally, we predicted that escorts would also preferentially respond to their associated pup's distress calls. We used pup distress calls rather than the much more frequently occurring begging calls for these experiments because distress calls are presumably used to attract adults and because, in pilot experiments, begging calls did not work very well in attracting escorts to the speakers.

METHODS

We studied a wild population of individually marked banded mongooses on and around Mweya Peninsular in Queen Elizabeth National Park Uganda (0°12' S, 29°54' E) between March 2004 and September 2005. For details on the study site and marking procedures see Cant (2000). The study population consisted of nine groups ranging from 5 to 60 individuals. Animals were classified as adults (> 12 months, sexually mature), subadults (6-12 months), infants (3-6 months) and pups (< 3 months). Pups are dependent on food provided by other group members, and adults as well as subadults may escort

pups. Six of the groups were habituated to observers following at a few meters distance and were included in the experiments described below.

Recordings

We recorded pup distress calls when the pups were trapped for individual marking at an age of between 25 and 53 days. Escort contact calls and pup begging calls (when pups were aged between 25 and 50 days) were recorded during foraging at 0.5 to 1 m distance from the caller (for spectrograms see Fig. 1). In 2004 we used a Sennheiser ME 66/K6 directional microphone connected to a Sony digital audio tape recorder (TCD-D100) and transferred the recordings onto a personal computer using an ESI Waveterminal U24. In 2005 we used a Marantz PMD670 audio recorder. All recordings were sampled at 48 kHz.

Acoustic analyses

Calls with a good signal-to-noise ratio were selected in Avisoft SASLab Pro 4.38 (R. Specht, Berlin, Germany) and call parameters were measured using Avisoft and LMA 2005 (K. Hammerschmidt, Göttingen, Germany). In total we measured 20 parameters for the distress and begging calls and 19 parameters for the contact calls (see Appendix A-C). Both programs offer a batch processing option, which enforces a degree of standardization missing when calls are analysed individually. Some relevant parameters could be measured in only one of the two programs whereas call duration and frequency of the first dominant frequency band (begging and distress calls) or quartile frequencies (contact calls) were measured by both programs. Calls were excluded if the values of one or more of these parameters differed by more than 5% between the measurements of the two programs. All measurements were done from spectrograms with FFT length 1024, frequency resolution 47 Hz and time resolution 1.33 ms (distress and begging calls) or 0.67 ms (contact calls). In total, we measured 20 distress calls from each of 12 pups of one litter (L1) and from eight pups of another litter (L2). Likewise, we measured 20 contact calls from each of eight adults from one group, all potential escorts. Since we could not obtain good recordings of distress and begging calls for enough individuals

within one litter, we measured distress and begging calls from each of 13 pups from six different groups (10 calls per call type and individual).

We used stepwise discriminant function analysis (DFA) in SPSS 13.0 to extract those variables from the original set of parameters which contributed to individual distinctness of calls (see Appendix). In one case, two highly correlated variables ($r>0.8$) were chosen by the DFA and the less distinctive of the two was excluded posthoc. We then determined the probability of assignment to the correct individual based on the discriminant functions using leave-one-out cross-validation. The found percentage was compared to correct assignment by chance (bootstrapping with 10,000 runs). The discriminant functions obtained for the begging calls were additionally used to individually assign distress calls from the same pups.

Parameters of begging and distress calls were compared using linear mixed models (LMMs) with the restricted maximum likelihood method and including individual as a random factor. Sex of the pup was included as an additional factor in the original model but dropped as none of the parameters differed significantly between sexes. Since 20 parameters were tested, the significance level was set to 0.0025.

Removal experiments

Removal experiments were performed after escorting associations had been stable for at least three days (meaning a pup's nearest adult for at least 70% of the time during foraging was the same on three consecutive days). Of all pup-escort pairs in a group, only those were tested for which good quality recordings of calls were obtained. Within this subset, we randomly chose focal pairs from which one partner was temporarily removed and its calls played back to the remaining partner, and control pairs from which one partner was removed at the same time but no calls were played back. Removals took place when the groups were foraging, between 0700 and 1100 or between 1600 and 1800 hours. Playback experiments were conducted on average 80 min (range 30-140 min) after the removal using the Sony/Marantz recorder and portable speakers (CREATIVE Travelsound). In total, we performed 13 pup removal and 12 escort removal experiments in six different groups. Pup-escort pairs were treated as statistical units. No individual pup or escort was tested twice as focal animal. However, three escorts and one pup served once as focal and, in another experiment, as control individual.

For the pup removal experiments, two pups that were in stable associations were removed concurrently. Removed individuals were put in a live-trap and carried away out of hearing range (> 500m). The speakers were hidden in a cardboard box and placed on the ground, partly camouflaged next to a bush. Playbacks of the focal pup's distress call were started when both the focal escort (escort of the pup whose calls were played back) and the control escort (escort of the pup that had also been removed but whose calls were not played back) were foraging or resting at equal distance from and within 15 m of the speakers. Control and focal escorts did not differ in age (Wilcoxon signed-rank test, $T=18$, $N=13$, $p>0.1$), weight (paired t-test, $t=0.13$, $N=11$, $p=0.90$, two individuals could not be weighed) and sex (six of 13 control escorts and seven of 13 focal escorts were males). We recorded latency to approach and time spent next to the speakers for the focal and the control individuals. Animals that came to within 1 m of the speakers were considered as having approached them. Playbacks of pup distress calls lasted 60 s and consisted of loops of 10 calls played repeatedly at 30 calls per min. The volume of the playbacks was set to 50-60 dB at 50 cm using a Voltcraft 329 sound level meter. This is about 5 dB above the naturally observed volume of these calls. Distress calls used for the playbacks had been recorded no more than 20 days prior to the experiments.

The same procedure was used for the escort removal experiments, during which two escorts were removed concurrently. We played back contact calls of the focal escort to the focal and control pups when they were at equal distance of the speakers. Each playback of the focal escort's contact calls was preceded by a control playback of contact calls of a non-escorting adult. Experimental playbacks were performed 10 min after the end of the control playbacks. We performed the control playbacks consistently before the experimental playbacks, rather than in random order, because a pup responding to the first playback might reduce its probability to respond to the second. Playbacks of adult contact calls lasted 180 s and consisted of loops of five calls played repeatedly at 15 calls per min. The volume of the playbacks was set to 40-45 dB at 50 cm (about 5 dB above the naturally observed volume of these calls). Contact calls used for the playbacks had been recorded no more than 4 months prior to the experiments.

For both experiments, if neither the control nor the focal individual had approached the speakers during the playback, it was started a second time 5 to 10 min later (four of the 13 'distress' and three of the 12 'contact' playbacks). During one 'distress' playback, neither the control nor the focal escort approached the speakers even at the second attempt and, thus, both individuals were recorded as having not responded

to the playback. In this case the focal adult visually responded to the first playback and started searching behaviour but failed to approach the speakers. Neither the focal nor the control escort responded to the second playback. Also during two 'contact' playbacks, neither pup approached the speakers at the second attempt. Response latency for individuals that did not approach the speakers during the playback was set to the duration of the playbacks (60 s for escorts during pup removals, 180 s for pups during escort removals).

RESULTS

Acoustic analyses

Pup distress calls

For the litter of twelve pups, stepwise DFA extracted nine parameters relevant for individual distinctiveness of the calls from the original set of parameters (see Appendix table A). With leave-one-out cross-validation, the corresponding nine discriminant functions assigned 75.4% of the calls to the correct individual (Fig. 2a), about eight times more than the 8.5 % expected by chance (bootstrapping, $p<0.0001$). For the litter of eight pups, 73.1% of the calls were correctly assigned, compared to 12.5% expected by chance ($p<0.0001$).

Escort contact calls

Stepwise DFA extracted six parameters relevant for individual distinctiveness of the contact calls from the original set parameters (see Appendix table B). With leave-one-out cross-validation, the corresponding six discriminant functions assigned 35.0% of the calls to the correct individual (Fig. 2b) which is 2.5 times more than the 12.5% expected by chance (bootstrapping, $p<0.0001$).

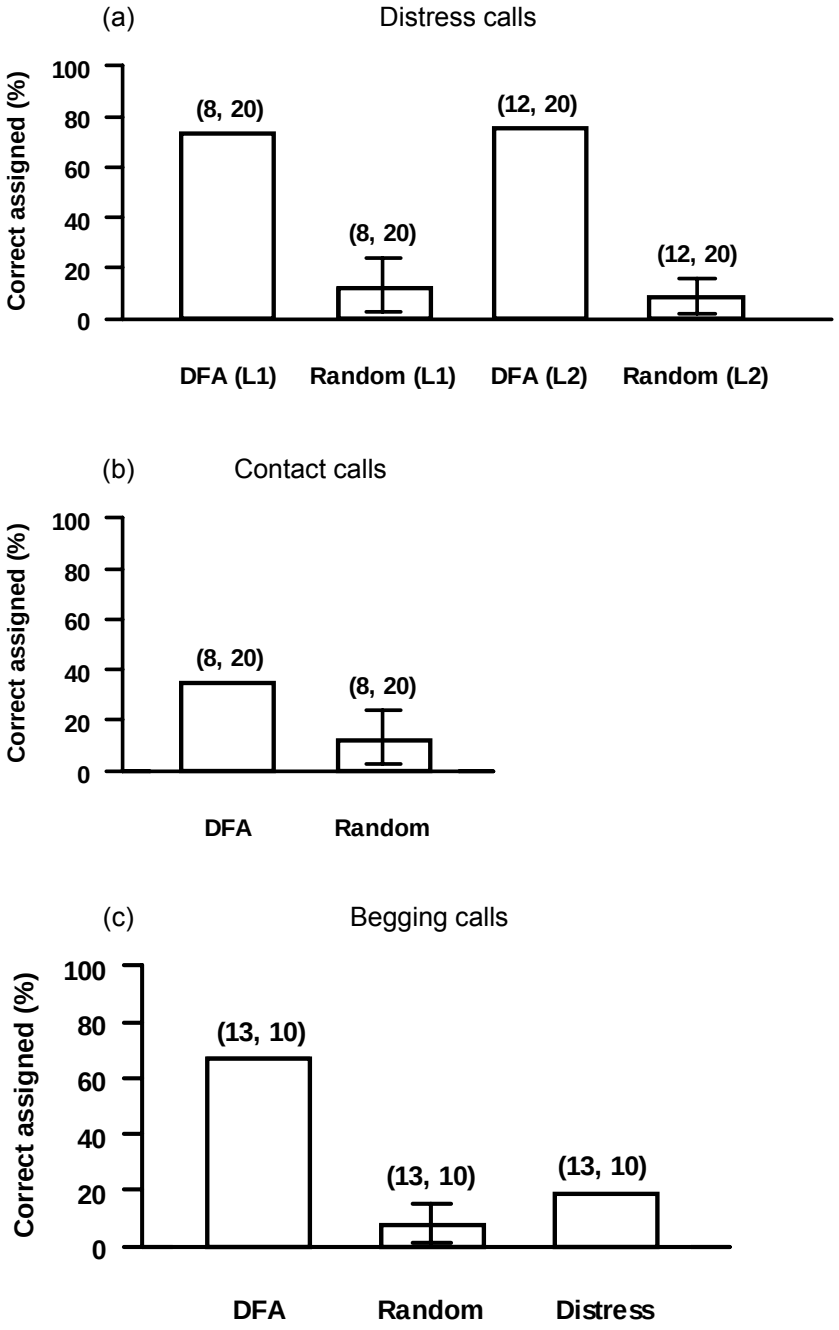

Figure 2. Percentage of calls assigned to the correct individual using DFA (leave-one-out cross-validation) and expected by chance (bootstrapping). (a) Pup distress calls for two different litters (L1 and L2) separately. (b) Adult contact calls. (c) Pup begging calls (with assignment of distress calls with discriminant functions based on begging calls shown on the far right). For assignment by chance, mean and 95% confidence limits are shown. Numbers in brackets give number of individuals and number of calls per individual.

Pup begging calls

For the begging calls, stepwise DFA extracted eight parameters relevant for individual distinctiveness of the calls (see Appendix table C). With leave-one-out cross-validation, the corresponding eight discriminant functions assigned 66.9% of the calls to the correct individual (compared to 7.7% expected by chance, $p<0.0001$; figure 2c). The same discriminant functions correctly assigned 19.2% of the distress calls of the same 13 pups (10 calls per pup; Fig. 2c). By bootstrapping, correct assignment by chance of 19.2% or more was reached in only 13 of 10,000 runs ($p=0.0013$). This probably underestimates the potential for correct assignment across call types, since distress and begging calls differed significantly in four of the eight parameters used in the discriminant functions (LMM with individual as random factor and correcting for age, all $p<0.0025$; see Appendix table D). Repeating the analysis with only parameters that did not differ between distress and begging calls (12 of the original set of 20 parameters) reduced the correct assignment rate for the begging calls (to 50.8%), whereas the correct assignment of the distress calls was slightly higher (21.5%).

Removal experiments

Pup removal

The focal escort approached the speakers during 12 of the 13 experiments, whereas the control escort approached during five of the experiments (Fisher test: $p=0.011$). The focal escorts were quicker to approach the speakers than the control escorts (Wilcoxon signed-rank test: $T=3$, $N=13$, $p<0.01$; Fig. 3a) and stayed longer near the speakers ($T=10$, $N=13$, $p<0.05$; Fig. 3b).

Escort removal

During the control playbacks of non-escort contact calls, two of 12 focal pups and one of 12 control pups approached the speakers (Fisher test: $p>0.5$). During the playbacks of escort contact calls, nine of the 12 focal pups and three of the 12 control pups approached the speakers (Fisher test: $p=0.039$). The focal pups were quicker to approach the speakers than the control pups (Wilcoxon signed-rank test: $T=1.5$, $N=12$, $p<0.01$; Fig. 3c) and stayed longer near the speakers ($T=5$, $N=12$, $p<0.05$; Fig. 3d).

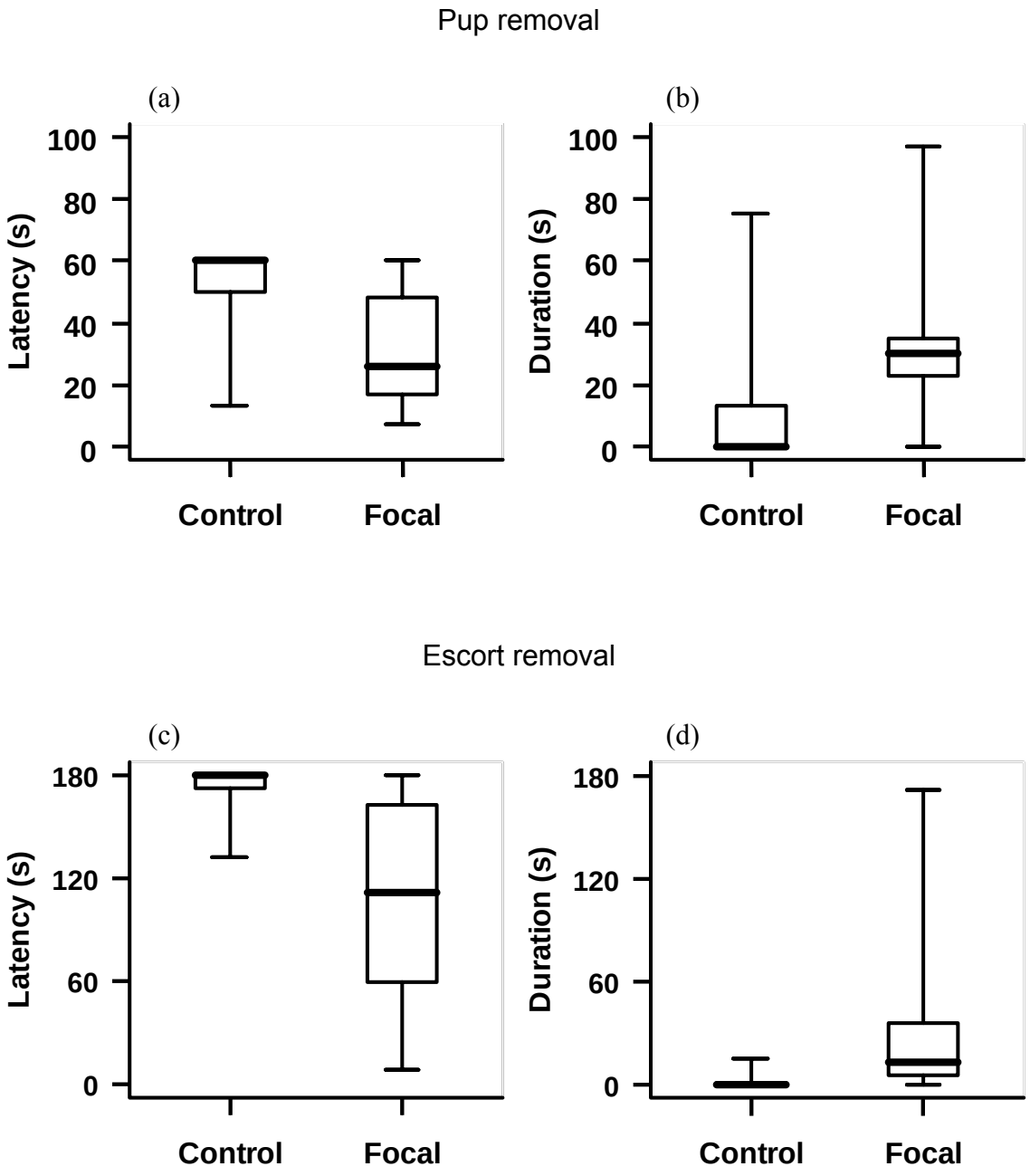

Figure 3. Responses of control and focal individuals to playback experiments. (a) Response latency to pup-distress playbacks. 60 s correspond to no approach. (b) Time spent within 1 m of the speakers during pup-distress playbacks. (c) Response latency to escort-contact playbacks. 180 s correspond to no approach. (d) Time spent within 1 m of the speakers during escort-contact playbacks. Shown are median, interquartile range and range.

DISCUSSION

We showed that the distress calls of banded mongoose pups as well as the contact calls of adults are individually distinct and that pups and escorts recognize each other by these vocalizations. We suggest that this is a case of true individual recognition of offspring by providers because age differences among pups were minimal (< 3 days), responses were not directed to individuals of a particular sex and differences in relatedness among pups within litters are probably small in this inbreeding species (Waldick et al. 2003). Furthermore, our experiments demonstrated that both pups and escorts play an active role in the maintenance of escorting associations. While the pups' benefits are well established (Gilchrist 2004; Hodge 2005), it is largely unclear how helpers benefit from these associations.

Adults responding preferentially to distress calls of their associated pups may be a consequence of the constant exposure to begging calls of these pups. This probably leads to hormonal changes in the exposed individuals (Carlson et al. 2006) and therefore escorts may be more responsive to distress calls of pups than non-escorts. Furthermore, even though escorts interact regularly with other pups, they are exposed to begging calls of one particular pup much more than to calls of other pups. Thus, escorts may be more responsive to distress calls of their associated pup because they are primed to calls of this individual (analogous to vocal identity priming in humans; Ellis et al. 1997). The escorts' preferential response to distress calls of their associated pups may therefore be a by-product of them being more familiar with vocalizations of this particular individual, rather than an adaptive response. Nevertheless, this leads to escorts contributing to the maintenance of the escorting associations.

An alternative and more intriguing possibility is that, in this species, escorts respond preferentially to distress calls of their associated pups because they benefit from stable associations with particular young. First, escorts may care preferentially for more closely related pups. There is evidence that breeders are more likely to escort pups than non-breeders (Gilchrist & Russell 2007). However, pedigrees are not available at this date and it is therefore unknown whether parents are more likely to escort one of their own rather than an alien pup. Also, even though multiple males and females are breeding concurrently, high levels of inbreeding and the consequent low genetic variability

(Waldick et al. 2003) within groups give little opportunity for helpers to dispense care in a kin-biased way. Furthermore, females within groups commonly give birth in synchrony in the same den (Cant 2000) and cues associated with kinship may therefore not be available in this system. Second, escorts may care for future coalition partners. Banded mongooses commonly disperse as single-sex factions which may include individuals of an age differing by several years (Cant et al. 2001). Therefore, same-sexed pup-escort pairs may end up in the same dispersing faction. However, there is little evidence that associations are preferentially formed with same-sexed partners (Hodge 2003; Gilchrist 2004) and, thus, this is unlikely to explain the adults' interest in forming escorting associations.

We believe the most likely explanation for escorting associations are group-augmentation benefits (Woolfenden 1975; Brown 1987; Kokko et al. 2001). In banded mongooses, both males and females often breed in their natal group (Cant 1998; Gilchrist 2001) and young adults of both sexes contribute substantially to pup care (Gilchrist 2004; Gilchrist & Russell 2007; Hodge in press). Escorts may therefore benefit from caring for future helpers which will later help raise their pups. Group size is also a crucial determinant of success in competition with neighbouring groups (Rood 1975; Cant et al. 2002). Pups and escorts forming close associations may be the most efficient way of raising offspring in this species, since escorted pups grow faster and are more likely to survive to independence than non-escorted pups (Hodge 2005). However, although a possible reason for helping in this species, group augmentation does not necessarily require escorting associations to be stable throughout the whole period of the pup's dependence unless escorts can increase the efficiency of care by monitoring the food intake of a particular pup. The long-term costs of escorting to an individual can be reduced if helpers take turns in escorting between breeding attempts. This is likely to be the case since helpers in good body condition give away more food and are thus more likely to escort pups (Gilchrist 2004; Gilchrist & Russell 2007), and individuals contributing heavily to care have temporarily reduced growth rates (Hodge 2003). Similarly, meerkat helpers that invest a lot in one breeding attempt reduce their effort in the next breeding attempt (Russell et al. 2003).

Mutual recognition of parents and offspring by acoustic means has been demonstrated in a variety of species (e.g. Espmark 1971; Insley 2001; Searby & Jouventin 2003). However, in some cases recognition is unidirectional with parents not recognizing their offsprings' calls (Falls 1982; Torriani et al. 2006). The distinction of

unidirectional and mutual recognition has been related to the mobility of offspring and anti-predator strategies (Torriani et al. 2006), with unidirectional recognition being predicted where offspring remain stationary and hide, such as in fallow deer (*Dama dama*), and mutual recognition where offspring follow their parents, such as in sheep (*Ovis aries*; Shillito-Walser et al. 1981; Searby & Jouventin 2003) and reindeer (*Rangifer tarandus*; Espmark 1971). Alternatively, unidirectional recognition may be explained by a low probability of confusion where offspring remain stationary and separated from conspecifics and, thus, spatial cues are reliable indicators of an individual's identity (Falls 1982). Instead, mutual recognition may be required where offspring mingle with each other, as for example in species breeding in colonies, forming crèches or living in groups with mobile offspring (see Appendix table E). Dependent banded mongoose pups follow adults during foraging (from an age of 3-4 weeks; Rood 1974; Cant 2003), mingle with other pups in the group and pups rely on adults for defence against predators. Mutual recognition in this species, thus, fits the predictions of the hider-follower hypothesis and the confusion hypothesis.

Pups clearly benefit from recognizing their escorts vocally since this accelerates the reunion process after temporal separation and therefore reduces the time during which little food is received and vulnerability to predators is high. Escorts may benefit from recognizing their associated pups if escorting reflects preferential care. Alternatively, recognition may be beneficial if it allows increasing the efficiency of provisioning either by reducing the time pups spend alone and the distance escorts have to travel to feed a pup or by escorts monitoring the amount of food the pups receive, which may be more reliable than using begging rate as a correlate of the pups' hunger level (Kilner & Johnstone 1997; Bell 2006).

Individual recognition of pups' distress calls is matched by high distinctiveness of these calls, particularly in parameters of frequency and frequency-modulation (see Appendix table A). Compared to the distress calls, adult contact calls were much simpler in structure and less individually distinct. Our finding that pups nevertheless successfully recognized the contact calls of their escorts indicates that a moderate assignment certainty of single calls is sufficient. This may be particularly true for repeated calls. Alternatively, we may not have measured some parameters relevant for individual recognition of these calls.

Since distress calls are emitted infrequently and pup vocalizations change significantly within a matter of a few weeks (12 of the 20 parameters changed

significantly with age, see Appendix table D), we hypothesized that escorts may use the much more frequently heard and structurally similar begging calls as templates for individual recognition of distress calls. The discriminant functions based on the acoustic structure of the begging calls assigned distress calls to the correct individual with a probability that was significantly higher than expected by chance. However, with roughly 20% (2.5 times higher than expected by chance for 13 individuals), the probability was still very low. This poor performance despite the apparent similarity of begging and distress calls (see Fig. 1) can partly be explained by significant differences between begging and distress calls in some of the parameters most important for correct assignment. More sophisticated approaches, as for example used recently by Reby et al. (2006) to assign calls to individuals across call types in red deer (*Cervus elaphus*), may show a higher potential of pup begging calls to serve as templates for recognition of other pup vocalizations.

Banded mongoose pups and escorts recognized each other acoustically and our experiments demonstrated that both parties contribute to the maintenance of the escorting associations. We offered two interpretations for the adults increased responsiveness to distress calls of their associated pup. First, it may be a by-product of the escorts being constantly exposed, and thus primed, to begging calls of this pup. Second, it may reflect preferential care for particular pups. This stands in contrast to observational data suggesting that escorts dispense care indifferently and feed the nearest pup on most occasions (Gilchrist 2004). It remains to be investigated what benefits escorts accrue from provisioning pups and whether these benefits require escorting associations to be stable over several weeks. Also, it remains unclear which role pups and escorts play in the initial formation of the associations.

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APPENDIX

Table A. Parameters used in the discriminant function analysis of pup distress calls.

Parameter*	Category	Program†
Start frequency of 1st dominant frequency band (DF)	Frequency	LMA
End frequency of 1st DF	Frequency	LMA
Maximum frequency of 1st DF	Frequency	LMA
Minimum frequency of 1st DF	Frequency	LMA
Mean frequency of 1st DF	Frequency	LMA
Factor of linear trend of 1st DF	Global frequency modulation	LMA
Alternation frequency between original curve and linear trend	Local frequency modulation	LMA
Maximum deviation from linear trend	Local frequency modulation	LMA
Minimum deviation from linear trend	Local frequency modulation	LMA
Number of changes between original and floating average curve	Local frequency modulation	LMA
Mean deviation from floating average	Local frequency modulation	LMA
Maximum deviation from floating average	Local frequency modulation	LMA
Duration of call	Temporal	LMA
Location of maximum amplitude	Temporal	Avisoft
Amplitude ratio between 1st and 2nd DF	Relative amplitude	LMA
Entropy at start	Entropy	Avisoft
Entropy at end	Entropy	Avisoft
Mean entropy	Entropy	Avisoft
Minimum entropy	Entropy	Avisoft
Maximum entropy	Entropy	Avisoft

* Parameters used for classification of both datasets are shown in bold, parameters used for classification in only one dataset are shown in italic.

† Software program used to measure the parameter.

Table B. Parameters used in the discriminant function analysis of adult contact calls.

Parameter*	Category	Program†
Maximum peak frequency	Frequency	LMA
Minimum peak frequency	Frequency	LMA
Mean peak frequency	Frequency	LMA
Mean frequency of 1st Quartile	Frequency distribution	Avisoft
Mean frequency of 2nd Quartile	Frequency distribution	Avisoft
Mean frequency of 3rd Quartile	Frequency distribution	Avisoft
Maximum frequency of 1st Quartile	Frequency distribution	Avisoft
Maximum frequency of 2nd Quartile	Frequency distribution	Avisoft
Maximum frequency of 3rd Quartile	Frequency distribution	Avisoft
Minimum frequency of 1st Quartile	Frequency distribution	Avisoft
Minimum frequency of 2nd Quartile	Frequency distribution	Avisoft
Minimum frequency of 3rd Quartile	Frequency distribution	Avisoft
Duration of call	Temporal	LMA
Number of pulses	Temporal	Avisoft
Pulse rate	Temporal	Avisoft
Mean pulse duration	Temporal	Avisoft
Mean interval between pulses	Temporal	Avisoft
Mean amplitude of 1st frequency peak	Relative amplitude	LMA
Max amplitude of 1st frequency peak	Relative amplitude	LMA

* Parameters used for classification are shown in bold.

† Software program used to measure the parameter.

Table C. Parameters used in the discriminant function analysis of pup begging calls.

Parameter*	Category	Program†
Start frequency of 1st dominant frequency band (DF) ‡	Frequency	LMA
End frequency of 1st DF	Frequency	LMA
Maximum frequency of 1st DF ‡	Frequency	LMA
Minimum frequency of 1st DF	Frequency	LMA
Mean frequency of 1st DF ‡	Frequency	LMA
Factor of linear trend of 1st DF	Global frequency modulation	LMA
Alternation frequency between original curve and linear trend	Local frequency modulation	LMA
Maximum deviation from linear trend ‡	Local frequency modulation	LMA
Minimum deviation from linear trend	Local frequency modulation	LMA
Number of changes between original and floating average curve ‡	Local frequency modulation	LMA
Mean deviation from floating average	Local frequency modulation	LMA
Maximum deviation from floating average ‡	Local frequency modulation	LMA
Duration of call	Temporal	LMA
Location of maximum amplitude	Temporal	Avisoft
Amplitude ratio between 1st and 2nd DF	Relative amplitude	LMA
Entropy at start	Entropy	Avisoft
Entropy at end	Entropy	Avisoft
Mean entropy ‡	Entropy	Avisoft
Minimum entropy	Entropy	Avisoft
Maximum entropy ‡	Entropy	Avisoft

* Parameters used for classification are shown in bold.

‡ These parameters differ significantly between begging and distress calls ($p<0.0025$).

† Software program used to measure the parameter.

Table D. Parameter values for distress and begging calls (based on 10 calls per individual and call type).

Parameter*	distress †	begging †	$F_{1, 245}$	p
Start frequency of 1st dominant frequency band (DF) ‡	6539 Hz	7980 Hz	156.5	<0.0001
End frequency of 1st DF ‡	3588 Hz	3641 Hz	1.12	0.29
Maximum frequency of 1st DF ‡	7001 Hz	8461 Hz	297.9	<0.0001
Minimum frequency of 1st DF ‡	3460 Hz	3596 Hz	3.46	0.064
Mean frequency of 1st DF	5106 Hz	6248 Hz	160.3	<0.0001
Factor of linear trend of 1st DF ‡	-0.356	-0.304	2.68	0.10
Alternation frequency between original curve and linear trend ‡	9.02	8.09	1.58	0.21
Maximum deviation from linear trend ‡	1168 Hz	1927 Hz	53.8	<0.0001
Minimum deviation from linear trend	341 Hz	376 Hz	3.10	0.079
Number of changes between original and floating average curve ‡	35.0	30.5	43.0	<0.0001
Mean deviation from floating average	70.7 Hz	58.4 Hz	6.47	0.012
Maximum deviation from floating average ‡	696 Hz	1043 Hz	12.1	<0.001
Duration of call	337.6 ms	384.5 ms	7.66	0.006
Location of maximum amplitude ‡	0.45	0.55	5.70	0.018
Amplitude ratio between 1st and 2nd DF	3.70	4.24	3.54	0.061
Entropy at start ‡	0.22	0.22	1.88	0.17
Entropy at end	0.31	0.30	2.24	0.14
Mean entropy	0.46	0.49	13.4	<0.001
Minimum entropy ‡	0.16	0.15	1.38	0.24
Maximum entropy	0.44	0.42	12.0	<0.001

* Parameters differing significantly between distress and begging calls (after Bonferroni correction) are shown in bold.

† Shown are mean values of 130 calls.

‡ Parameters that were influenced significantly by the age of the pup (range: 25-53 days). Sex of the pup did not influence any of the parameters and was thus excluded from the model.

Table E. Overview of studies showing uni-directional or mutual vocal recognition between parents and offspring. Only studies with experimental evidence are shown.

Species	Context	Recognition	Reference	Method
Fallow deer	hider species	parents do not recognize young	Torriani et al. 2007	Playback
Laughing gull	young stay near nest	parents do not recognize chicks	Falls 1982	Playback
Reindeer	herd with mobile offspring	mutual	Espmark 1971	Playback
Sheep	herd with mobile offspring	mutual	Searby & Jouventin 2003	Playback
Northern fur seal	colony breeding	mutual	Insley 2001	Playback
Adélie penguin	colony breeding	mutual	Falls 1982, Jouventin & Aubin 2002	
Ancient murrelet	colony breeding, precocial	mutual	Jones et al. 1987	Playback
Cliff swallow	colony breeding	mutual	Stoddard & Beecher 1983, Beecher et al. 1985	Playback
Barn swallow	not colony breeding	parents do not recognize nestlings	Medvin & Beecher 1986	Playback & cross-f.
Common murre	colony breeding	mutual	Falls 1982	Playback
Razorbill	nests more widely separated than in common murre	parents do not recognize chicks at age 4 d but do so at age 10 d	Falls 1982	Playback
Pinion jay	fledglings form crèches	mutual	Falls 1982	Playback
Bank swallow	fledglings form crèches	parents recognize fledglings	Falls 1982	Playback
Rough-winged swallow	fledglings do not form crèches	parents do not recognize fledglings	Falls 1982	cross-fostering
Manx shearwater	burrow breeding	chicks do not recognize parents	Falls 1982	Playback

References (not including those given in the main reference list): Jouventin & Aubin 2002, Anim. Behav. 64: 747ff.; Jones et al. 1987, Anim. Behav. 35: 1405ff.; Stoddard & Beecher 1983, Auk 100: 795ff.; Beecher et al. 1985, Auk 102: 600ff.; Medvin & Beecher 1986, Anim. Behav. 34: 1627ff.

Table F. Values of two individually distinct parameters of pup distress calls and of one individually distinct parameter of adult contact calls (discussed in General Discussion, pp. 137-138)

Table 1. Two parameters important for the individual distinctness of pup distress calls. Shown are mean ± SE of 20 calls per individual.

Individual	Df1mean (Hz)	Df1chmean (Hz)
1	5316 ± 83	292 ± 29
2	4325 ± 99	241 ± 22
3	3898 ±77	293 ± 28
4	5548 ±183	335 ± 39
5	4658 ± 136	269 ± 29
6	4352 ± 135	176 ± 17
7	4676 ± 138	379 ± 34
8	5728 ± 125	189 ± 19
Statistic	$F_{7,152}=26.6$ *p<0.0001*	$F_{7,152}=6.0$ *p<0.0001*

Df1mean: mean frequency of first dominant frequency band.
Df1chmean: mean deviation of first dominant frequency band from floating average curve.

Table 2. Duration of adult contact calls for eight individuals. Shown are mean ± SE of 20 calls per individual.

Individual	Duration (ms)
1	36 ± 1
2	57 ± 4
3	37 ± 1
4	52 ± 3
5	48 ± 2
6	39 ± 1
7	43 ± 1
8	42 ± 2
Statistic	$F_{7,152}=11.7$ *p<0.0001*

CHAPTER 4

The information banded mongooses extract from heterospecific alarms

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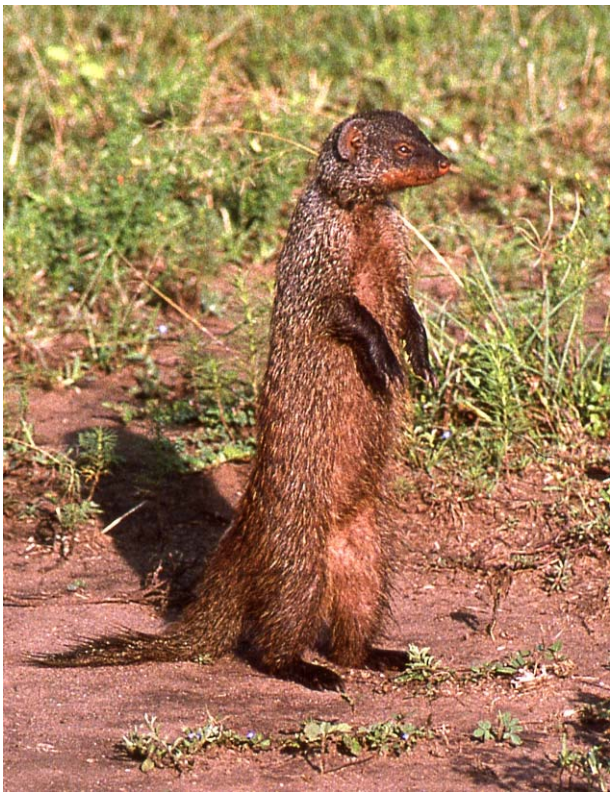

The information banded mongooses extract from heterospecific alarms

Corsin A. Müller* & Marta B. Manser

Verhaltensbiologie, Zoologisches Institut, Universität Zürich, Winterthurerstrasse 190, 8057 Zürich, Switzerland

ABSTRACT

Predation is a powerful selective force shaping the behaviour of prey animals. As a consequence, a variety of birds and mammals have developed referential and/or urgency-based alarming systems. Since anti-predator behaviour is likely to be costly, it should pay to attend to warning signals given by other species. Evidence that animals respond to heterospecific alarm calls is abundant. However, studies showing whether animals extract information on predator types or urgency level from heterospecific alarms are rare. Using playback experiments, we investigated whether banded mongooses (*Mungos mungo*) respond to alarm calls of several sympatric plover species (*Vanellus* sp.), and how mongooses respond to plover alarms that differ in their level of urgency. Banded mongooses responded to alarm calls of all three plover species tested. Even though the response intensity varied over a large scale, the responses to plover alarms did not differ between calls representing high and low urgency. The response intensity was not influenced by the rate at which the mongoose groups were naturally exposed to alarms of the respective plover species. Our results indicate that banded mongooses use heterospecific alarms for predator avoidance but do not use additional information provided in these signals. This might be related to low costs of responding to these alarms and also to how recognition of heterospecific alarms is acquired.

INTRODUCTION

Predation pressure is a powerful selective force shaping morphology and behaviour of prey animals (Lima & Dill 1990; Zuberbühler 2000b). A widely studied consequence are sophisticated alarming systems in birds and mammals (reviewed in: Macedonia & Evans 1993; Bradbury & Vehrencamp 1998; Searcy & Nowicki 2005). Many species communicate not only the presence of predators with their alarm calls, but the calls additionally include information about urgency, predator type and/or predator size (Macedonia & Evans 1993; Manser et al. 2001; Templeton et al. 2005). Since anti-predator behaviour is likely to be costly (Pulliam 1973; Dimond & Lazarus 1974; Sherman 1977, 1985), it should pay animals that share common predators to exploit the vigilance of sympatric species and respond to their alarm calls. This may increase the probability of escaping a predator (Morse 1977) and may allow to reduce the own vigilance in favour of other activities.

Responses to heterospecific alarm calls have been demonstrated in a variety of species, in particular birds, rodents and primates (reviewed in: Fichtel 2004; Randler 2006). However, little is known about how attentive animals are to categorical and continuous information encoded in heterospecific alarms, such as predator types or urgency. A few recent studies have demonstrated that animals can extract information on predator types and predator size from heterospecific alarms (Zuberbühler 2000b; Fichtel 2004; Rainey et al. 2004; Templeton & Greene 2007). It can thus be predicted that animals also respond appropriately to the urgency level of heterospecific alarm calls, particularly because urgency level is more likely encoded in a consistent way across species than referential information (Morton 1977; Fichtel et al. 2001; Manser et al. 2001; Fichtel & Hammerschmidt 2002).

How recognition of heterospecific alarms is acquired is not clear. It has been suggested that recognition is acquired by associative learning (Curio 1971; Nuechterlein 1981; Hauser 1988; Shriner 1999), or that alarm calls are recognized by acoustic properties common to alarm calls across taxa (Marler 1957; Bradbury & Vehrencamp 1998). If associative learning plays a role, the response should be correlated with the rate at which heterospecific alarms are encountered. In contrast, no such relationship is expected if heterospecific alarms are recognized by their acoustic properties. The

mechanism by which recognition is acquired my also limit the amount of information that can be extracted from heterospecific alarms, with associative learning allowing more differentiated responses (for example to referential information) than recognition by acoustic properties.

We studied responses to heterospecific alarms in banded mongooses, *Mungos mungo*, small (<2 kg) group-living carnivores. In the study area, banded mongoose groups share their home ranges with several plover species, but mongooses and plovers do not aggregate. Even though direct predation was not observed, mongooses and plovers are likely to share predators, in particular large raptors such as martial eagles (*Polemaetus bellicosus*; Boshoff et al. 1990). Natural observations suggest that banded mongooses respond to crowned plover, *Vanellus coronatus*, alarm calls and that these calls vary with level of urgency (personal observation).

We investigated whether banded mongooses respond to alarm calls of plovers and whether responses differ depending on urgency levels encoded in the plovers' alarms. We recorded alarm calls of crowned plovers given to humans at different distances and determined whether call rate and call duration change with distance to perceived threat, which was taken as a correlate of urgency. We also recorded alarm calls of the banded mongooses themselves to test whether their calls change in a similar way with urgency. Additionally, we recorded alarm calls of two other plover species, spurwinged plovers, *Vanellus spinosus*, and wattled plovers, *Vanellus senegallus*. We then played back the alarm calls of the three plover species (for spectrograms see Fig. 1a-d) to banded mongoose groups to show that they respond to heterospecific alarms. We further tested whether the response intensity is related to the rate at which the groups are naturally exposed to alarm calls of the respective plover species. Finally, we conducted playback experiments varying two features of high and low urgency alarm calls of crowned plovers, call rate and call duration. We predicted that the mongooses would react more intensely to the plovers' high urgency calls than to the low urgency calls.

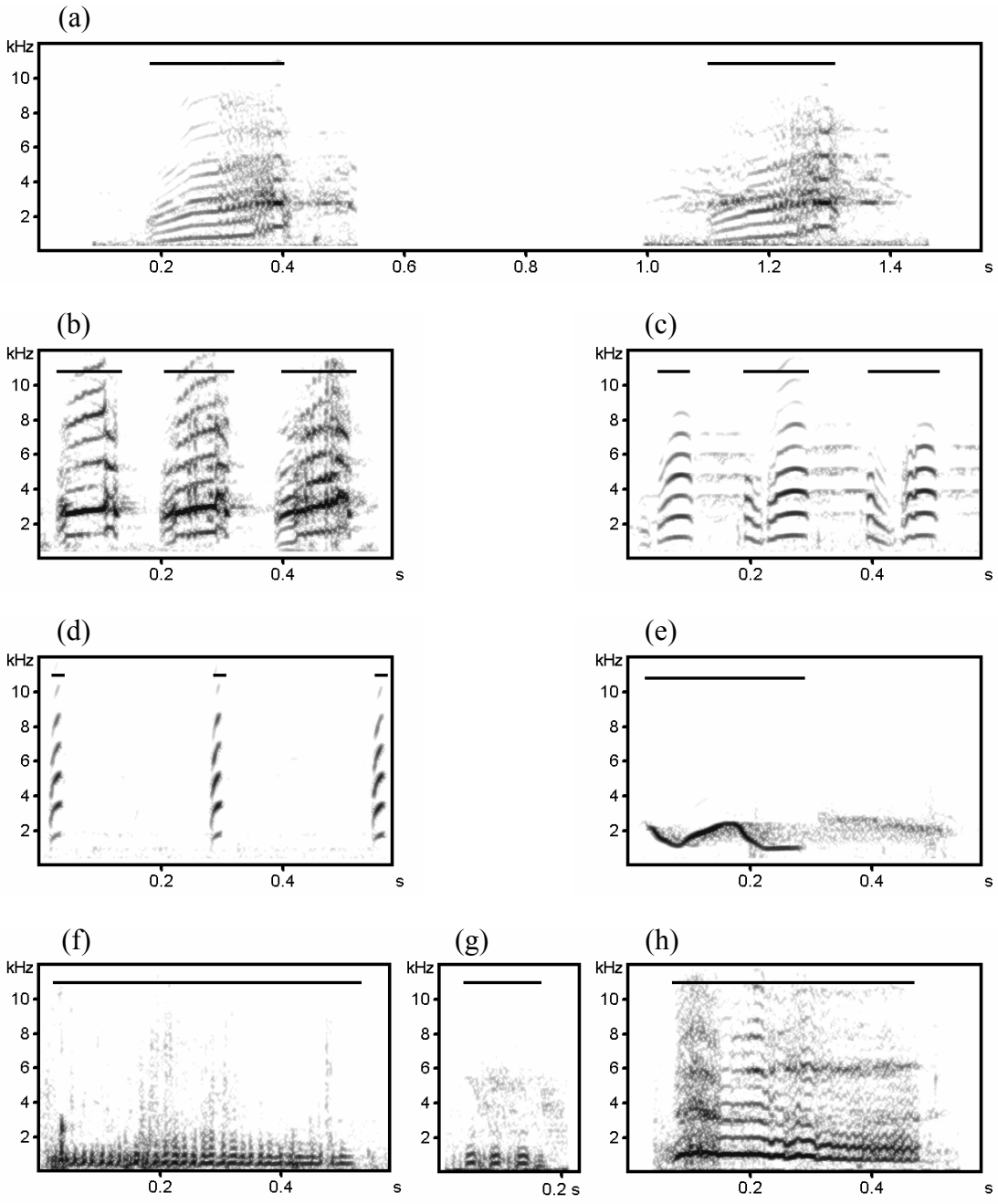

Figure 1. Spectrograms of alarm calls (FFT length: 512, frequency resolution: 47 Hz, time resolution: 1.33 ms) created in Avisoft SASLab Pro 4.38 (R. Specht, Berlin, Germany). Horizontal bars denote single calls detected with a threshold of -15 dB to the maximum amplitude and a hold time of 20 ms. (a) Crowned plover alarm calls (low urgency). (b) Crowned plover alarm calls (high urgency). (c) Wattled plover alarm calls. (d) Spurwinged plover alarm calls. (e) Black-headed gonolek duet call (used for control playbacks). (f) Banded mongoose low urgency alarm call. (g) Banded mongoose high urgency alarm call. (h) Banded mongoose panic call.

METHODS

We studied a wild population of individually marked banded mongooses on and around Mweya Peninsular (8 km^2) in Queen Elizabeth National Park, Uganda (0°12' S, 29°54' E; for details on the study site see Cant 2000) between August 2004 and September 2005. The study population consisted of 251 individuals in eight groups. Group size ranged from 8 to 60 individuals. Animals were classified as adults (>12 months), subadults (6-12 months) and infants (<6 months). Groups were habituated to close observation and all animals were trapped on a regular basis to refresh individual marks (colour-coded plastic collars or small shaves on the rump), detect pregnancies, take morphometric measures and estimate ectoparasite load. Procedures followed the guidelines of the Association for the Study of Animal Behaviour and are described in detail elsewhere (Cant 2000). Data on each group's exposure to plover alarms were collected during regular visits to the groups and are presented as alarms per observation hour (observation time per group: mean 240 hours, range 117-354 hours).

Audio Recordings

We recorded 33 alarms of crowned plovers and 21 alarms of banded mongooses given in response to a moving human. This procedure has the advantage over using naturally occurring alarms in that the stimulus can be kept constant. Plover alarms were given to a person stepping out from behind a large bush at varying distances (10-57 m) and were recorded by the person representing the threat stimulus. The same procedure was used to obtain banded mongoose alarms (distance 6-37 m), except these alarms were recorded by a sitting observer (2-10 m from the alarming individual) and a second person represented the stimulus. This difference in the procedure was necessary because plovers were not habituated to a close observers and mongoose alarms were too faint to be recorded from a large distance. Distance between the threat and the alarming individual was determined using a Leica rangefinder (LRF 800). The stimulus was presented equally often at short, medium and long distance for both species. For the mongooses, distance was also balanced within groups. Eight more crowned plover alarms were obtained at long distances (>30 m) but with distance only estimated by eye. These calls were used for

playbacks but not included in the correlation of call parameters with distance. Alarms of spurwinged plovers and wattled plovers were obtained only for short distances to the threat (8 recordings of each species). Additionally, we recorded duet calls of 15 black-headed gonoleks, *Laniarius erythrogaster*, for use in control playbacks (for spectrogram see Fig. 1e). Gonolek calls were chosen because they are conspicuous but non-threatening stimuli, which are similar to plover alarm calls in length and low between-call variation in the acoustic structure. All recordings were sampled at 48 kHz. In 2004 we used a Sennheiser ME 66/K6 directional microphone connected to a Sony digital audio tape recorder (TCD-D100) and transferred the recordings onto a personal computer using an ESI Waveterminal U24. In 2005 we used a Marantz PMD670 audio recorder.

Alarm calls of crowned plovers and banded mongooses were analysed for urgency-related differences. Only initial alarms (the first alarm given by any group member) were used in the analysis. Plover alarms consisted of repeated calls (see Fig. 1a and b) of which the average duration and average call rate over the first five calls was used in the analysis. Mongoose alarms were single calls (see Fig. 1f and g). Call duration and call rate of alarm calls were measured to the nearest millisecond in CoolEdit 2000 (Syntrillium Software Corporation, Scottsdale, AZ, U.S.A.). Of crowned plover alarm calls, peak frequency at the maximum amplitude was the only frequency parameter that could be measured reliably (in Avisoft SASLab Pro 4.38, R. Specht, Berlin, Germany; FFT length: 1024, frequency resolution: 47 Hz, time resolution: 0.67 ms). Frequency parameters of banded mongoose alarm calls could not be analysed due to poor recording quality.

Since plovers were not individually recognizable and the identity of the alarming mongooses could not be determined on all occasions, it cannot be ruled out that some individuals contributed more than one alarm to the dataset. Recordings of the same bird species were separated spatially by at least 100 m. This reduced the likelihood that individual plovers were recorded repeatedly since all three plover species were breeding in the study area and individuals spent most of the time in limited areas close to the nest (personal observation). It is unlikely that individual mongooses contributed more than one alarm to the dataset because initial alarms calls were typically given by the first individual to spot the danger and no particular individuals were much more likely to alarm than others (personal observation). We thus treated separate recordings as independent.

Editing of Playbacks

The amplitude of plover alarm calls was standardized in CoolEdit and playbacks with a standardized call rate (high call rate: 120 calls/min, low call rate: 20 calls/min) were compiled. Each playback consisted of ten calls and included three to five calls played in a loop, which corresponds to a duration at the lower edge of naturally occurring alarms. The set of calls was obtained from a different recording for each playback. Crowned plover alarms were categorized as low urgency if given to a threat (human observer) at more than 30 m distance without flying off and as high urgency if given to a threat at less than 20 m distance while flying off. Differences between high urgency and low urgency calls may communicate distance to threat. Alternatively, the differences between these calls may be related to the act of flying off (Trillmich et al. 2004). In both cases, information about urgency is available to receivers due to consistent differences in the calls between the two contexts.

Of each of the three plover species, a playback sequence with high urgency calls at the high call rate was prepared. For crowned plovers, we additionally prepared playbacks with high urgency calls at the low call rate and playbacks of low urgency calls at both call rates, resulting in six different plover playbacks (Table 1). Control playbacks (gonolek calls) matched experimental playbacks in duration, volume and call rate.

Playback Experiments

Eight groups of banded mongooses (mean size excluding infants = 22.5) were exposed to the six plover playbacks, which were conducted using the Marantz recorder and portable speakers (CREATIVE Travelsound). Plover playbacks to the same mongoose group were spaced at least seven days apart. We set playback amplitude to 65 to 70 dB at 50 cm from the speakers using a Voltcraft 329 sound level meter. The speakers were placed on the ground, 8 to 12 m from the nearest individual. Playbacks were only started when more than half the group had been foraging for at least 15 min and no alarm had occurred during this period. Since banded mongooses often foraged in thick bush, a handful of bait (20-50 g of a mix of rice and gravy) was used to persuade them to forage on open ground, which allowed direct observation of the responses. This amount of food was generally consumed within 1 to 2 min and playbacks were started

after this period. Clumped food sources like this also occur naturally, for example in the form of piles of elephant dung infested with insect larvae. Experiments were conducted between 0800 and 1100 hours and between 1630 and 1830 hours. Each playback of plover alarms was preceded (mean 7 min, range 5-20 min before) by a playback of gonolek calls. This allowed to control for baseline vigilance, which may vary depending on recent exposure to predators or presence of pups. Since we had obtained only 15 recordings of gonoleks, we randomly choose one of these for use as a control in each of the 48 experiments (Table 1). The response of individuals foraging within 20 m of the speakers was recorded using a digital video camera (Panasonic NV-GX7). Anti-predator behaviour during the playbacks was determined for every individual visible on the tape (mean 11.5, range 4-23 individuals). We recorded lookup rate, lookup duration (determined frame by frame in Windows Movie Maker, Microsoft Corp., U.S.A.; 1 frame = 0.08 s) and moving towards cover. Lookups were defined as interrupting an activity and raising the head abruptly above shoulder level. Since the mongooses went back to normal foraging immediately after the end of the playbacks, we only analysed the behaviour until 3 s after the last played plover call. Infants hardly ever responded to the playbacks and were not included in the analyses. In each experiment, a different sub-sample of the group (mean 58%, range 10-100% of all individuals) was visible on the videotape. Thus, most individuals contributed to the measured response during several experiments, but some did not. Since we videotaped the responses with a wide angle to include a large number of individuals, we could not read the individual identities reliably. We therefore analysed the response to the playbacks at group level, assuming that the individuals visible on the videotape were a representative sample of the group.

Statistical Analyses

Call rate, call duration and peak frequency of crowned plover alarms were analysed in an analysis of variance, treating every recording as an independent data point. Duration of banded mongoose alarm calls as well as anti-predator behaviour of mongoose groups during the playbacks were analysed using linear mixed models (LMMs) with the residual maximum likelihood method and group identity included as a random factor. The occurrence of alert behaviour (raise on hind legs and/or move to cover) was analysed in a

Generalized Linear Mixed Model (GLMM) with binomial error structure and a logit link function.

Table 1. Treatments of alarm call playbacks

		Urgency			
		High	Medium	Medium	Low
	call rate	high	high	low	low
	call duration	short	long	short	long
Species	CR	*N*=8 (11.8, 5-18)	*N*=8 (10.9, 5-20)	*N*=8 (13.9, 6-19)	*N*=8 (10.6, 5-21)
	WA	*N*=8 (9.5, 4-14)	-	-	-
	SP	*N*=8 (12.0, 8-17)	-	-	-

CR: Crowned plover, WA: Wattled plover, SP: Spurwinged plover. Each treatment was preceded by a control playback of gonolek calls with the matching call rate. *N* gives the number of mongoose groups tested. Numbers in brackets give mean and range of number of animals that were visible on the videotapes. Mean and range for the control playbacks were 11.6 and 4-23 individuals.

We scored response intensity of the mongoose groups to the playbacks as the average proportion of time that individuals engaged in anti-predator behaviour (lookup and/or move to cover) during the playbacks. The duration of anti-predator behaviour was recorded for every individual visible on the video tape and then averaged over all individuals. Response intensity thus increased when more individuals responded and/or when individuals showed anti-predator behaviour for a longer time. Proportions were arcsine-transformed to attain normality and analysed in a LMM, controlling for the presence of pups (present during 21 of the 48 experiments). To account for the

widespread group-size effect on anti-predator vigilance (Lima & Dill 1990), the number of individuals visible on the videotape was taken as a measure of how many individuals were nearby. This slightly underestimates the relevant measure of foraging aggregation size (Blumstein 1996), but it is more accurate than social group size since banded mongoose may spread out considerably during foraging and spend much time invisible to each other in thick bush (personal observation). Social group size did not influence the responses to the playbacks (p-values for the main effect and all interactions were larger than 0.1) and was dropped from the models. Responses to plover playbacks were additionally controlled for vigilance intensity during the control playbacks. Data analysis was carried out in R 2.2.1 (R Development Core Team 2005).

RESULTS

Alarm Calls and Urgency

We obtained 33 alarming bouts of crowned plovers for which distance to threat was known. Plover behaviour and distance to threat explained a large proportion of the variance in call rate (r^2=0.79) and average duration of calls (r^2=0.59) but not of peak frequency (r^2=0.06). Alarms of plovers flying off had a higher call rate ($F_{1,30}$=107.6, P<0.0001; Fig. 2a) and were shorter ($F_{1,30}$=41.0, P<0.0001; Fig. 2b) than alarms of plovers remaining sedentary. After controlling for this, call rate decreased with distance to threat ($F_{1,30}$=8.57, P=0.006), whereas the duration of calls did not increase significantly with distance to threat ($F_{1,30}$=2.10, P=0.16). Peak frequency could be determined reliably for only 26 of the recordings and was influenced neither by plover behaviour ($F_{1,23}$=0.10, P=0.75) nor by distance to threat ($F_{1,23}$=1.27, P=0.27).

We recorded 21 alarm calls given by banded mongooses from six groups in response to approaching humans. The duration of these alarm calls was positively correlated with distance to threat (LMM, $F_{1,14}$=106.9, P<0.0001; Fig. 2c). At very close distances (<8 m), a structurally different call was given (panic call, Fig. 1h). Initial alarms were always single calls. Repeated calls were sometimes given after retreat from the threat.

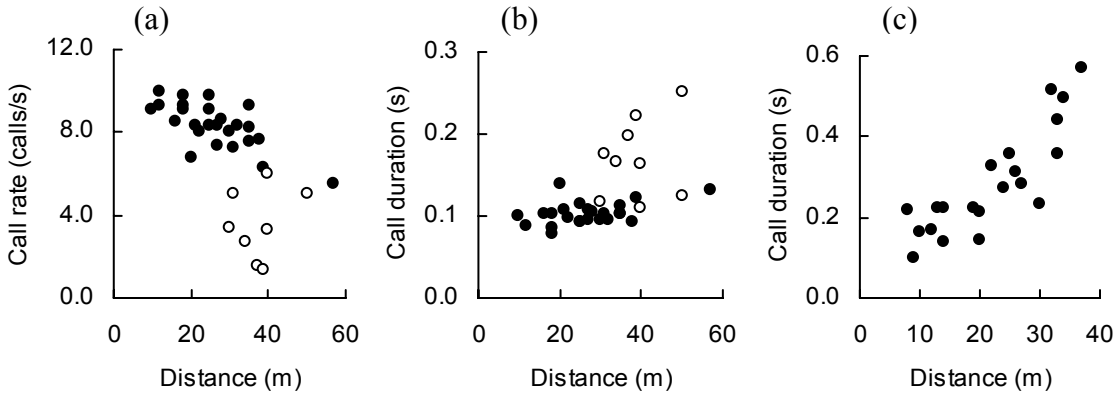

Figure 2. Temporal characteristics of alarm calls of crowned plovers and banded mongooses varied with distance to perceived threat. (a) Call rate of crowned plover alarms. (b) Duration of crowned plover alarm calls. ●: Plovers flying off while alarming. ○: Plovers remaining sedentary while alarming. (c) Duration of banded mongoose alarm calls.

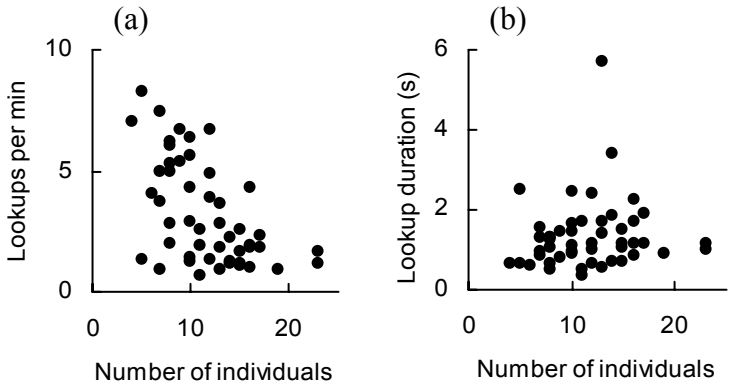

Figure 3. Vigilance behaviour of banded mongooses as a function of number of individuals nearby. (a) Lookup rate per individual. (b) Average lookup duration.

Response to Calls of Different Species

During control playbacks (gonolek calls), mongooses spent on average 10.3% (SE=1.4%, *N*=48 experiments) of the time with vigilance behaviour. The average lookup rate per individual decreased with increasing number of individuals nearby (LMM, $F_{1,37}$=6.53, *P*=0.015; Fig. 3a), whereas average lookup duration did not change (LMM on log transformed data, $F_{1,37}$=0.05, *P*=0.83, Fig. 3b). The presence of pups influenced

neither lookup rate nor lookup duration (lookup rate: $F_{1,37}$=0.003, P=0.96; lookup duration: $F_{1,37}$=0.04, P=0.84). Both measures also did not change with the rate at which gonolek calls were played back (lookup rate: $F_{1,37}$=0.78, P=0.38; lookup duration: $F_{1,37}$=0.07, P=0.79).

Mongoose groups responded to the high urgency plover playbacks with increased vigilance compared to control playbacks and sometimes retreated to cover. Mongoose groups spent more time with anti-predator behaviour (lookup and/or move to cover) during the playbacks of plover alarm calls compared to the gonolek playbacks (LMM, $F_{1,35}$=37.1, P<0.0001; Fig. 4a). This response was not dependent on which plover species was played back. However, the increase in anti-predator behaviour was highest during spurwinged plover playbacks, intermediate during wattled plover playbacks and lowest during crowned plover playbacks (species*treatment interaction: $F_{2,35}$=3.04, P=0.06). Alert behaviour of at least one individual (raise on hind legs and/or move to cover) was observed during 11 of the 24 high urgency playbacks whereas only during one of the control playbacks an individual showed alert behaviour (GLMM, $F_{1,37}$=10.7, P=0.002). Mongoose alarm calls were observed on one occasion, during a wattled plover playback.

The mongooses' response to the plover playbacks was not influenced by how often groups were naturally exposed to alarms of the plover species played back (LMM, $F_{1,11}$=0.11, P=0.75), even though exposure rates varied over more than an order of magnitude (Fig. 4b). Excluding the extreme value (exposure 2.6 alarms per hour) did not change this result. Differences in the response intensity to the alarms of the three plover species were not significant ($F_{2,11}$=3.43, P=0.07), and neither did the presence of pups influence the response intensity ($F_{1,11}$=0.03, P=0.87).

Response Depending on Urgency

We tested whether the responses differed between playbacks of crowned plover alarms of varying urgency. The calls used for the playbacks differed in duration between high and low urgency treatments (averages over calls per playback, high urgency: $X \pm$ SE = 90.6 ± 3.0 ms, low urgency: $X \pm$ SE = 172.4 ± 14.2 ms; t test for unequal variances: $t_{7.6}$=5.6, P=0.001). The response to playbacks was not influenced by the call rate at which crowned plover alarms were played back (LMM, $F_{1,20}$=0.41, P=0.53; Fig. 5). However, mongoose groups reacted more strongly to playbacks of long (low urgency) alarm calls

than to those of short (high urgency) alarms (proportion anti-predator behaviour: long calls $X \pm SE = 0.357 \pm 0.108$, short calls $X \pm SE = 0.183 \pm 0.037$, $F_{1,20}=5.28$, $P=0.03$; Fig. 5). No interaction between call rate and call duration was detected ($F_{1,20}=0.63$, $P=0.44$) and the response to the playbacks was not influenced by the presence of pups either ($F_{1,20}=0.04$, $P=0.85$).

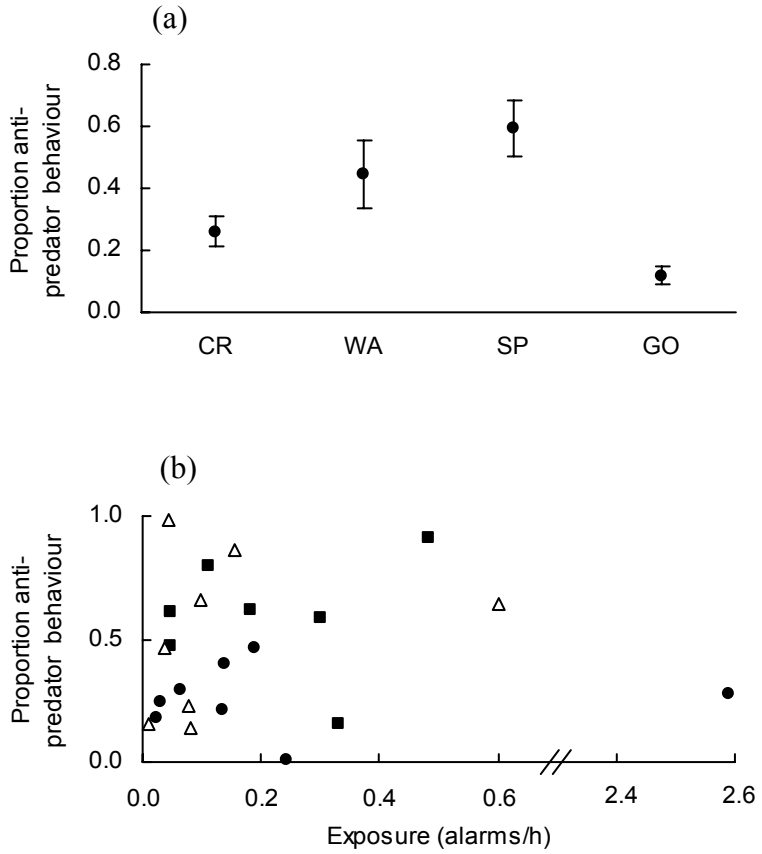

Figure 4. Proportion of time spent with anti-predator behaviour during playbacks of plover alarm calls for eight banded mongoose groups. (a) Response to alarm calls of crowned plovers (CR), wattled plovers (WA) and spurwinged plovers (SP), and to control playbacks of black-headed gonolek duet calls (GO). Mean ± SE are shown. (b) Proportion anti-predator behaviour as a function of exposure rate to naturally occurring alarms of the respective plover species. ●: Crowned plover alarms. ∆: Wattled plover alarms. ■: Spurwinged plover alarms.

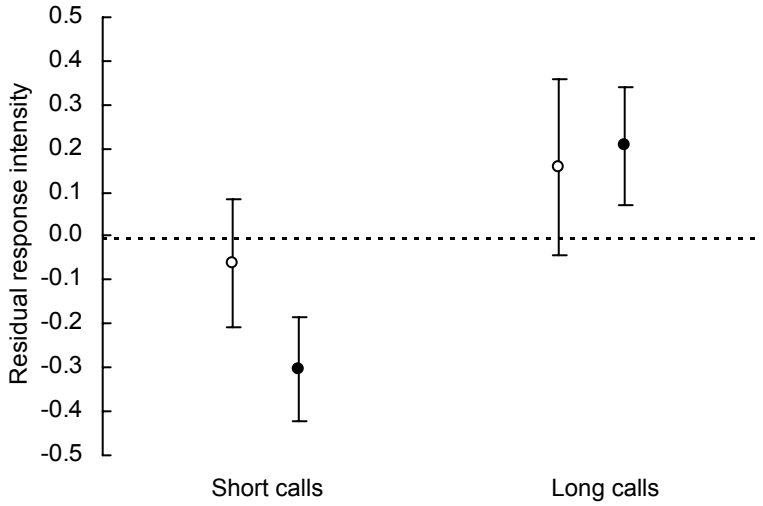

Figure 5. Response intensity of eight banded mongoose groups to playbacks of short and long crowned plover alarm calls at a low call rate (●) and at a high call rate (○). Shown are residuals of a LMM controlling for vigilance during the control playback and including group identity as a random factor. Mean ± SE are given.

DISCUSSION

Banded mongoose groups responded to playbacks of plover alarm calls with increased vigilance compared to playbacks of non-threatening songbird calls and sometimes retreated to cover. This response is qualitatively equivalent to the mongooses' response to conspecific alarm calls observed in natural situations (personal observation). The mongooses responded to alarm calls of all three plover species, yet the response intensity tended to differ among the three plover species. This effect may be attributable to differences in fundamental frequency, frequency modulation and/or syllable duration of alarm calls among plover species (see Fig. 1b-d), which may make the calls of one species more salient to mongooses than the calls of the other species. For example, a sensory bias might make the detection of spurwinged plover calls more likely because of their steeper frequency modulation (Vallet & Kreutzer 1995).

The intensity of the responses to plover alarms was not related to the rate at which the respective mongoose group was exposed to alarms of the plover species even though, for some mongoose groups, exposure rate to alarm calls of the three plover species varied markedly. This suggests that either exposure rates of less than 0.05 alarms per hour are

sufficient to allow associative learning, or that the mongooses attend to common acoustic features shared by alarm calls of different species (Marler 1957; Stefanski & Falls 1972; Johnson et al. 2003). This could be tested by playing back alarm calls of a non-native plover species to banded mongooses (Ramakrishnan & Coss 2000; Fichtel 2004). Mongooses may also learn to recognize alarm calls of the bird species they are exposed to most frequently and then generalize to other species they are exposed to less often, thus combining associative learning and recognition of alarms by their acoustic properties. Alternatively, banded mongooses may learn to react to heterospecific alarms by a different mechanism such as observational conditioning (Heyes 1994), which may not require as high exposure rates as associative learning, or selective habituation (Deecke et al. 2002), which is independent of the exposure rate to the alarm calls.

Banded mongoose groups did not respond to playbacks of crowned plover alarms according to urgency of the alarms, even though temporal characteristics of both the plovers' and the mongooses' alarm calls varied with distance to perceived threat. The consistent variation in crowned plover alarms potentially allows other species to estimate the urgency level even if crowned plovers do not use an urgency-based alarming system themselves. However, banded mongooses may not be attentive to changes in the call rate of alarm calls because they do not give repeated calls for initial alarming themselves. More surprising was our finding that the mongooses neither responded to crowned plover alarm calls according to the urgency level encoded in the duration of the calls, even though the duration of banded mongoose alarms changed in a similar way with distance to threat. On the contrary, banded mongooses responded more intensely to longer crowned plover alarm calls (representing lower urgency), possibly because longer calls represented stronger stimuli. However, we do not know whether banded mongooses use urgency-related differences in their own alarm calls since, due to the poor recording quality, we were not able to do playback experiments with conspecific alarm calls. Also, we cannot exclude that banded mongooses use parameters other than call duration to encode urgency in their alarm calls and, therefore, do not respond to urgency-related differences in either call rate or call duration of plover alarms.

Individual banded mongooses decreased their vigilance during control playbacks with increasing number of group members in their vicinity. This group-size effect on vigilance has been demonstrated in many vertebrate species, in particular in birds and ungulates (reviewed in: Elgar 1989; Quenette 1990; Roberts 1996; Treves 2000) and is thought to allow for increased foraging efficiency (Pulliam 1973). It remains to be shown

whether banded mongooses also decrease vigilance when foraging in the presence of plovers, which would represent a direct benefit of attentiveness to heterospecific alarm calls.

Banded mongoose groups responded to playbacks of heterospecific alarm calls but not according to the simulated level of urgency. Recent studies have shown that animals may extract referential information from heterospecific alarms (Zuberbühler 2000b; Fichtel 2004; Rainey et al. 2004). Banded mongooses not attending to urgency-based differences in bird alarm calls suggests that at least some species may respond to heterospecific alarms in a more crude way without using additional information encoded in these alarms. Use or lack of use of additional information may be related to the costs of correct and wrong responses and to how recognition of heterospecific alarms is acquired. Brief scanning is probably of little cost and therefore it may pay to respond to heterospecific alarms of low and high urgency equally, particularly since not responding may have fatal consequences. Conversely, referential information in alarm calls usually elicits different escape strategies (Seyfarth et al. 1980; Zuberbühler 2000a; Manser et al. 2001; but see Fischer & Hammerschmidt 2001) and ignoring this information in both conspecific and heterospecific alarms may lead to an inappropriate response with possibly lethal consequences. Therefore animals may be more likely to pay attention to referential than to urgency-related information in heterospecific alarms. Also, plovers being early warners, situations that are perceived by the plovers as high or low urgency may both represent only moderate urgency for the mongooses. Finally, the correct use of referential information in heterospecific alarms is probably acquired by associative learning (Zuberbühler 2000b; Fichtel 2004; Rainey et al. 2004). Other mechanisms of acquiring the use of heterospecific alarms, including observational conditioning, selective habituation and recognition of alarms by their acoustic properties, may be less likely to result in differentiated responses to heterospecific alarms.

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GENERAL DISCUSSION

General Discussion

In the preceding four chapters, I addressed questions of basic cognition that are directly or indirectly related to particular aspects of the social system or ecological environment of free-living banded mongooses. I showed what information individuals extract from their environment, but I also described situations where they either did not perceive or did not use available information. In this concluding chapter, I first discuss my findings with respect to limits to perception and ignorance of irrelevant information. The topics of the four chapters are quite dissimilar, ranging from communication within groups to between-group communication and use of heterospecific signals, and including olfactory and vocal communication. Therefore, I am first going to discuss each chapter separately, showing what information is used and not used, respectively and why this might be so. I will then discuss my results with regard to the mongooses' social system and give some suggestions for future research on cognition in this species.

Limits to the use of information

Neighbour recognition

I found that banded mongoose groups discriminate between neighbouring groups and strangers as well as between different neighbouring groups on the basis of scent marks (Chapter 1). Scent marks and excrements in particular are composite signals consisting of many components which are related to the producer's metabolism. They therefore include species-specific and probably also group- and/or individual-specific signatures (Ralls 1971; Thiessen & Rice 1976), which are partly explained by differences in diet (Beauchamp 1976; Ferkin et al. 1997), hormonal state and bacterial community (Müller-Schwarze & Mozell 1977). These signatures can be used to distinguish between friendly group-members and more or less dangerous foreigners. It is not surprising that banded mongooses extract this valuable information from secondary cues, given the olfactory acuity of carnivores (Gazit et al. 2005; Hepper & Wells 2005).

Even though banded mongooses discriminated between different neighbouring groups, I did not find the response intensity to be related to the size of the neighbouring group whose scent marks I presented. Quantity discrimination has been demonstrated in several bird and mammal species (Boysen 1997; Uller et al. 2001; West & Young 2002; Kilian et al. 2003). However, accurate discrimination is generally restricted to small numbers (< 10), whereas banded mongoose groups range in size up to 60 individuals. It is therefore unlikely that mongooses count the members of neighbouring groups. Also, in terms of threat levels, differences between two neighbouring groups of varying size may be small compared to the distinction of neighbouring groups and strangers. Therefore, the absolute size of neighbouring groups may be irrelevant to residents, or it may lead to only subtle differences in the response. Rather than absolute sizes, banded mongooses are expected to discriminate relative sizes, namely between groups that are larger or smaller than the own group, particularly since this determines the outcome of fights between neighbouring groups (Cant et al. 2002). A rigorous test would require that each group is tested with scent marks of a smaller as well as a larger neighbouring group. This was not possible here since only one group of the study population shared a border with both a larger and a smaller group.

Scent-marking and intrasexual competition

Scent-marking is not only involved in competition between neighbouring groups but additionally serves other functions. This is accommodated in Chapter 2, which deals with the role of scent-marking in intrasexual competition. I showed that banded mongooses extract information about sex, age, dominance status and reproductive status of the sender from scent marks. Such information about members of neighbouring groups or transient strangers is valuable for the assessment of dispersal opportunities. For example, evicted females may be more likely to leave the natal group permanently, rather than trying to regain acceptance (Cant et al. 2001; Gilchrist 2006), if in neighbouring groups adult subordinate males are available with which they could found a new group. Within groups, monitoring the reproductive status of females is probably crucial for mate-guarding males and for females competing for breeding opportunities.

Even though differential responses demonstrated that banded mongooses can extract information about sex, age and dominance from scent marks, this did not lead to behavioural changes in all cases. This was particularly obvious when comparing the

response to samples of dominant and subordinate individuals. Differential inspection of dominant and subordinate samples was restricted to receivers of one sex in several cases and no differential response in the vocalizations elicited by the scent marks was found. Therefore, the information about dominance status of the marking individual may only be relevant in certain contexts. For example, dominant and subordinate individuals of foreign groups may be, overall, equally threatening to residents. On the other hand, samples of dominant females from neighbouring groups may be particularly interesting to resident males because they may offer options for extra-group matings (Cant et al. 2002), whereas in the case of strangers, typically transients, the distinction between dominant and subordinate females may be less relevant.

Individual recognition and escorting

I found that banded mongoose pups and their escorts recognize each other vocally (Chapter 3). Analysing the acoustic structure, I found that measures of frequency and frequency modulation were most important for the individual assignment of pup distress calls (see Chapter 3, Appendix A) and measures of frequency and frequency distribution as well as temporal parameters for adult contact calls (see Chapter 3, Appendix B). A large number of studies with a variety of species have investigated the acoustic structure of vocalizations and most have found them to be individually distinct (but see Torriani et al. 2006). However, it is discussed only rarely whether the observed differences among individuals are within the limits of the receiver's sensory system. Indeed, concrete values of differences among individuals in acoustic parameters important for individual distinctness of calls are often not reported (e.g. Lessells et al. 1995; Reby et al. 1998; Illmann et al. 2002; Soltis et al. 2005; but see Jouventin & Aubin 2002; Searby & Jouventin 2003). Therefore, I discuss some of the parameters I found to be potentially used for individual recognition with regard to limits of mammals' auditory capacities. Since carnivores, with the exception of domestic cats, are rarely studied in this regard, I use auditory limits of rodents and primates for reference.

Mean frequency of the first dominant frequency band was the most discriminant parameter of distress calls among individual banded mongoose pups. Mean measures per individual ranged from 3.9 to 5.7 kHz (see Chapter 3, Appendix F). Limens of frequency discrimination at 5 kHz range from 20 to 200 Hz in primates (Wienicke et al. 2001) whereas for rats the minimal difference perceived lies at about 300 Hz (Talwar &

Gerstein 1999). Also cats, though not tested at 5 kHz, can learn to discriminate sounds differing by 500 Hz (Brown et al. 2004) from a baseline frequency of 8 kHz. It is therefore likely that banded mongooses can use the observed frequency differences to assign calls to individuals.

Another important parameter for individual distinctness of distress calls was local frequency modulation, namely the mean deviation of the first dominant frequency band from the floating average. The limits to perception of frequency modulation can be compared across species using 'Weber ratios' calculated as twice the frequency deviation from the mean divided by the frequency of the mean ($2*\Delta f/f$). Limits to perception for rodents were found to lie at ratios between 0.035 and 0.063 (Heffner et al. 1971), whereas limits can be substantially lower in humans, bats and dolphins (<0.01; Esser & Kiefer 1996). Ratios varied between 0.02 and 0.45 for all distress calls measured. Therefore, even if banded mongooses cannot discriminate between calls of varying local frequency modulation, at the least they are able to tell apart calls which are perceived as modulated or not modulated.

Call duration was one of the most important parameters for individual distinctiveness of contact calls of adult banded mongooses. Mean duration per individual ranged from 36 to 57 ms (see Chapter 3, Appendix F). For sounds of short duration (100 ms), limits of time resolution in two rodent and three primate species were found to lie at differences in duration between 31 and 73 ms, whereas the limit is somewhat lower, at about 15 ms, in humans (Kelly et al. 2006). Since the maximum difference found between the mean duration of contact calls of two individuals was only 21 ms, I suggest that this parameter, even though individually distinctive, is probably not used for individual recognition of contact calls in the banded mongoose. Instead, measures of frequency distribution may be used for that purpose.

Even though pup distress and begging calls were found to be individually distinct, I did not detect sex-specific differences in any of the 20 parameters measured (see Chapter 3, Appendix D). It is therefore possible that banded mongooses cannot distinguish between male and female pups solely on the basis of their calls. The absence of sex-specific information in the pups' calls may restrict the potential for sex-preferential feeding since feeding decisions are likely based on the acoustic signal of begging calls (Kilner & Johnstone 1997). This finding coincides with the apparent absence of preferential care for pups of one sex in the banded mongoose (Gilchrist 2004; Hodge 2005).

Responses to heterospecific alarms

Banded mongooses showed anti-predator behaviour in response to alarm calls of several sympatric plover species, but not to other, non-threatening bird calls (Chapter 4). However, banded mongooses did not seem to attend to differences in plover alarm urgency. They did not respond more intensely to playbacks of alarms signalling high urgency in either call rate or call duration. The differences in call rate (20 vs. 120 calls/min) and call duration (90 vs. 170 ms) are well above the typical limit of temporal resolution of acoustic signals in mammals (Kelly et al. 2006). Therefore, limits of the sensory system probably do not account for the absence of a difference in the response intensity. I suggest that either the urgency differences communicated in the plover alarms are not relevant to the mongooses, or the mechanism by which recognition of heterospecific calls is acquired constrains how detailed information can be extracted from these calls.

Environmental knowledge and the banded mongooses' social system

Advanced cognitive abilities are commonly seen as a consequence of a cognitively challenging ecological or social environment (Byrne & Whiten 1988). Therefore, it is worth to discuss cognitive abilities in the social or ecological context that promoted their evolution. While I did not study higher cognitive abilities such as perspective taking or causal reasoning, my study nevertheless relates to the mongooses social and ecological environment.

Neighbour recognition and scent-marking

Banded mongooses compete within groups for breeding opportunities and food, but at the same time they cooperate in territory defence against aggressive neighbours. This requires discrimination of conspecifics on several levels, as demonstrated in Chapter 1. Neighbour recognition itself is not a task only social animals are confronted with. Indeed most studies on this topic were performed on non-social birds and mammals (reviewed in Temeles 1994). However, life in social groups influenced the outcome of neighbour-stranger discrimination in the banded mongoose. Also, discrimination in social animals may require more complex processes than in solitary animals since multiple

individuals have to be distinguished and assigned to the respective groups. This task could be considerably simplified if scent marks contain group-specific information. The social system of the banded mongoose puts further emphasis on the monitoring of neighbouring groups since these not only represent a threat, but also opportunities for dispersal. Monitoring size and composition of neighbouring groups is relevant for both sexes since in the banded mongoose both sexes are known to leave their natal group (voluntarily or forced; Cant et al. 2001) and take over other groups (Gilchrist 2001). In other social carnivores, the same may only be relevant for males, since they are the only sex to disperse and take over elsewhere, as for example in meerkats (Doolan & Macdonald 1996) or lions (Hanby & Bygott 1987; Pusey & Packer 1987). It may be even less relevant in species where dispersing individuals found new groups but do not take over existing ones, as is probably the case in naked mole rats (Braude 2000).

Individual recognition and escorting

The unusual pup care system of the banded mongoose, in which pups form stable associations with providers, requires true individual recognition (Chapter 3). The same ability may not be required in other cooperative breeders where helpers dispense care indiscriminately or solely based on categories such as sex or kinship (Komdeur 1994; Lessells 2002). In the closely related and also cooperatively breeding meerkat, adults do not discriminate between begging calls of pups of the own and other groups and individual recognition of pups' begging calls is therefore unlikely in this species (Manser pers. comm.). While this may be due to low individual distinctness of pups' begging calls in meerkats (Kunc & Manser pers. comm.), it may also reflect the difference in the pup care system between species. Unlike banded mongooses, meerkat pups do not form associations with particular adults and feeders do not seem to care preferentially for particular individuals (Brotherton et al. 2001). The absence of an individual-specific response may therefore also be explained by feeders treating individual pups equally. The presence or absence of individual recognition of pups by providers may thus be related to the feeding strategies that providers of a given species use.

Responses to heterospecific alarms

Finally, recognition of heterospecific vocalizations (Chapter 4) is probably advantageous for solitary as well as for social animals. However, it can be interpreted as a

form of ecological intelligence. Animals challenged with the difficult task of avoiding multiple predators and finding enough food for survival and reproduction at the same time do well extending their attention to signals of heterospecifics sharing the same task. Since predators differ in the threat they represent depending on species, size, distance and behaviour (Templeton et al. 2005; Edelaar & Wright 2006), and since different predator species often use specific hunting strategies (e.g. Boesch & Boesch 1989; Kullberg 1995; Cresswell et al. 2004), it should be beneficial to gather as much information on a specific threat as possible. Information encoded in conspecific as well as in heterospecific alarms then allows to take appropriate and efficient action (Zuberbühler 2000a, b). While the lack of use of urgency-related information in heterospecific alarms by the mongooses asks for an explanation, observations suggest that banded mongooses have knowledge about different predators. Martial eagles for example, one of the main aerial predators at the study site, invariably elicit strong responses whereas African fish eagles, raptors of similar size but specialized on other prey species, often only elicit a short glance and no alarm (pers. obs.). Discrimination of predators, knowledge about their hunting strategies and accurate estimation of distances as well as correct interpretation of cues indicating the presence of predators are therefore probably a consequence of a life in a complex biotic environment and particularly relevant for animals exposed to a wide range of predator types.

Conclusions and directions

I investigated what information banded mongooses extract from their environment on the basis of several examples of olfactory and acoustic communication. I showed several cases in which information was used, but also some in which available information was not used. Banded mongooses differentiated between neighbours and strangers as well as between different neighbours on the basis of scent marks, but they did not respond according to the size of neighbouring groups. They further extracted information about sex, age and social status from these scent marks, but this information in some cases did not lead to a behavioural change in the investigating individual. Pups and providers recognized each other individually by vocal means but the same mechanism probably does not allow discrimination of male and females pups. Finally, I

demonstrated that banded mongooses recognize heterospecific alarm calls, but they did not use information about the level of urgency encoded in these alarms.

I discussed why in some cases information is not used. First, the information may simply not be available. Second, the information may be available but can not be perceived by a limited sensory system. Third, information may be perceived, but this does not lead to any behavioural change since it is only relevant in a certain context. Finally, cognitive constraints may restrict the use of information that is available. I further discussed my results in relation to the banded mongooses social system. I argued that the dispersal system and the strategy for pup care in this species promoted cognitive abilities beneficial for these tasks, in particular discrimination among neighbouring groups, which is the basis for monitoring dispersal opportunities, and individual recognition of pups by their vocalizations, which is the basis for the observed escorting associations between individual pups and providers. Recognition of heterospecific alarm calls and discrimination between scent marks of varying sex, age and status on the other hand may be basic cognitive abilities that are not related to social life but beneficial to any mammal for avoiding predators and finding mates.

This study dealt with cognitive abilities of a social carnivore but far from exhaustively so. Banded mongooses offer a number of opportunities to study other, more advanced cognitive abilities. For instance, individual recognition being established, the associations between pups and providers may also be recognized by other group members, which would be an example of recognition of third-party relationships. Furthermore, banded mongooses sometimes use extractive foraging techniques which may favour the evolution of technical intelligence. For example, a common food source are insect larvae that protect themselves with a hard shell of mud during pupation. Some mongooses manage to crack these shells with their teeth, using an appropriate biting angle. However, many do not and an alternative strategy employed often is to smash the object against a hard surface such as a rock, a piece of wood or, if neither is available, the head of a conspecific (pers. obs.). The use of such techniques may lead to a basic understanding of causal relationships (Byrne 1997). Finally, competition for food within groups is intense and attempts to steal large food items from other group members are observed regularly (pers. obs.). Therefore, banded mongooses may benefit from using strategies that reduce the vulnerability to theft. For this task, the ability to take the perspective of competitors, the basis for deception, may be advantageous. Thus, banded

mongooses still offer a variety of opportunities to study cognition in a carnivore with a complex, and in some regards peculiar social system.

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I am much indebted to my supervisor Marta Manser, who gave me the opportunity to follow my ideas with much freedom and without the hassle of having to organize funding several times anew. I was also lucky to have her as an enthusiastic (sometimes even overly so) advisor who invested a lot of time into discussions and polishing of manuscripts even though I kind of fell out of her main line of interest. I am also grateful to Mike Cant, Robert Seyfarth and Carel van Schaik for their willingness to sacrifice their time and act as experts for my thesis.

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I got a lot of help during field work but also in logistics from Francis Mwanguhya and Solomon Kyabulima, our two dedicated field assistants. I learned much from their

professional work and enthusiasm. It is truly amazing that one can leave the project for a few months and, upon returning, find the individual marks of all mongooses fresh, all new-born pups marked and habituated and life history up to date. I do not think anybody can claim to have better field assistants than that. Apart from being a great help in the field, Francis and Solomon also became friends, not to say brothers, who entertained me marvellously during and after field work. Quiz: Who knows what a mongoose is doing when it is 'cowardizing'?

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make use of that), including, identity card, driver's licence and bank cards. Wonders are happening in Uganda, too!

Numerous people have read and commented on chapters of my thesis, which is highly appreciated: Sarah Hodge, Hansjörg Kunc, Neil Jordan, Claudia Fichtel, Alina Rusu, Linda Hollén, Andy Radford, Andrea Weidt, Peter Pearman, Barbara König, Matt Bell and Jason Gilchrist. Do not try to read any significance into the order the names appear in, it is randomized. Furthermore, I am grateful to Anna Lindholm for sitting down numerous times with me to discuss English issues and polish style. I always came out of her office happy with some ideas for more elegant wording. All the remaining mistakes and awkward formulations are there because I failed to seek her advice.

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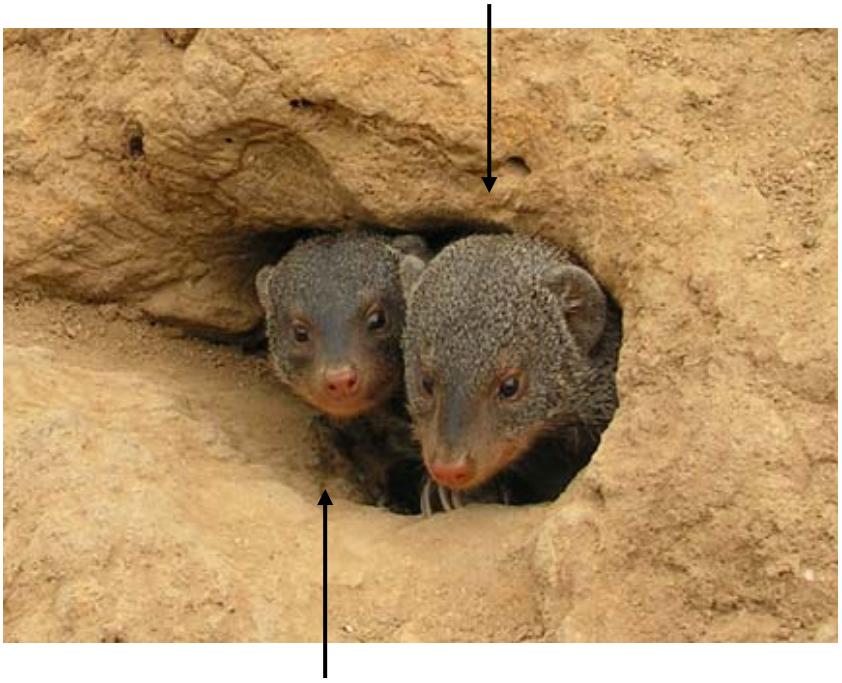
Some people have started the vice of thanking their study animals. I am not going to follow suite. Instead, I add a picture to acknowledge that I immensely enjoyed my time with the mongooses in Mweya.

According to people in Mweya this is Matt Bell, His Royal Mongooseness…



…and this is me, Crown Prince of the Mongeeses.

Curriculum Vitae

Personalien

Name	MÜLLER
Vornamen	Corsin Andreas
Geburtsdatum	17.10.1977
Bürgerort	Bütschwil SG

Ausbildung

1992-1997	Gymnasium Immensee, Matura Typus B
1997-2000	Studium in Biologie/Zoologie an der Universität Zürich
2000-2002	Diplomstudium am Zoologischen Institut der Universität Zürich. Titel der Diplomarbeit: 'Erhöhter Fortpflanzungserfolg durch Vermeidung von Spitzenbelastungen bei laktierenden Hausmäusen'. Leitung: Prof. Dr. Barbara König.
2003-2007	Promotion am Zoologischen Institut der Universität Zürich unter der Leitung von Prof. Dr. Marta Manser. Titel der Dissertation: 'Environmental knowledge in the banded mongoose (*Mungos mungo*)'.